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Movement of Resident Rainbow Trout Transplanted below a Barrier to Anadromy

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ARTICLE

Movement of Resident Rainbow Trout Transplanted below a Barrier to Anadromy

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Abstract

We tracked the movement of resident coastal rainbow trout *Oncorhynchus mykiss irideus* that were experimentally transplanted below a migration barrier in a northern California stream. In 2005 and 2006, age-1 and older rainbow trout were captured above a 5-m-high waterfall in Freshwater Creek and individually marked with passive integrated transponder tags. Otolith microchemistry confirmed that the above-barrier trout were the progeny of resident rather than anadromous parents, and genetic analysis indicated that the rainbow trout were introgressed with cutthroat trout *O. clarkii*. At each of three sampling events, half of the tagged individuals ($n = 22$ and 43 trout in 2005 and 2006, respectively) were released 5 km downstream from the waterfall (approximately 10 km upstream from tidewater), and an equal number of tagged individuals were released above the barrier. Tagged individuals were subsequently relocated with stationary and mobile antennae or recaptured in downstream migrant traps, or both, until tracking ceased in October 2007. Most transplanted individuals remained within a few hundred meters of their release location. Three individuals, including one rainbow trout released above the waterfall, were last detected in the tidally influenced lower creek. Two additional tagged individuals released above the barrier were found alive in below-barrier reaches and had presumably washed over the falls. Two of seven tagged rainbow trout captured in downstream migrant traps had smolted and one was a presmolt. The smoltification of at least some individuals, coupled with above-barrier “leakage” of fish downstream, suggests that above-barrier resident trout have the potential to exhibit migratory behavior and to enter breeding populations of steelhead (anadromous rainbow trout) within the basin.

The rainbow trout *Oncorhynchus mykiss* is characterized by populations of both resident and migratory forms, and migratory forms undergo runs either to the sea (anadromous) or wholly within freshwater (potamodromous) (Neave 1944). Individuals of a particular life history type frequently predominate in a river or stream (Moyle 2002). For example, along the west coast of North America, individual fish in populations of coastal rainbow trout *O. mykiss irideus* are generally anadromous and known as steelhead. However, resident rainbow trout often co-occur with migratory individuals within the same watershed,

a phenomenon referred to as partial migration (Jonsson and Jonsson 1993). Partial migration has been documented as well within other salmonid species, including sockeye salmon *O. nerka* (Ricker 1938), cutthroat trout *O. clarkii* (Hutchings and Morris 1985), Arctic char *Salvelinus alpinus* (Nordeng 1983), Atlantic salmon *Salmo salar* (Power 1958), and brown trout *S. trutta* (Jonsson 1985).

Partial migration may represent phenotypic plasticity within a common gene pool or result from fixed differences between sympatric but reproductively isolated populations. Over a broad

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geographic range in North America, the majority of genetic studies that compare sympatric populations of steelhead and resident rainbow trout have supported the former explanation (McPhee et al. 2007). Irrespective of life history type, genetic affinities have been found to be primarily associated with geographic proximity and genetic history (Docker and Heath 2003; Olsen et al. 2006; McPhee et al. 2007). A few studies have reported some level of genetic divergence between the two life history types of rainbow trout (e.g., Narum et al. 2004 in one of two Washington rivers; Docker and Heath 2003 in one of five river basins in British Columbia). Pearse et al. (2009) found that resident rainbow trout originating above a waterfall in a coastal California stream established a below-barrier subpopulation at the base of the falls that is genetically differentiated from a sympatric steelhead population. Genetic divergence and reproductive isolation between resident and anadromous salmonids may arise within a watershed through spatial or temporal segregation, or both, of spawning activity (Kurenkov 1978; Leider et al. 1984; Zimmerman and Reeves 2000; McMillan et al. 2007), assortative mating (Foote and Larkin 1988), out-of-basin stocking (Narum et al. 2004), or as a result of physical barriers such as waterfalls (Pettersson et al. 2001; Thrower et al. 2004a; Deiner et al. 2007, Pearse et al. 2009). Genetic divergence between resident and anadromous populations is likely to be greater in locations where physical barriers are relatively old and natural than in locations that have recently established barriers (Deiner et al. 2007).

Behnke (2002) argued that some amount of gene flow between coexisting resident rainbow trout and steelhead is likely in almost all settings, and that unambiguous genetic differentiation between the two life history types will be difficult or impossible to establish. Gene flow can arise, for example, because steelhead populations typically contain a small proportion of mature male parr that mature sexually without having smolted, and they might then mate as “sneakers” with resident females (e.g., Seamons et al. 2004; McMillan et al. 2007). For this reason, Behnke (2002) contended that conclusions about reproductive isolation and resolution of the fundamental question of whether “like gives rise to like” (i.e., steelhead producing only anadromous progeny and resident rainbow trout producing only resident forms) are better addressed with approaches that are not exclusively based on statistical analysis of data from genetic markers.

A few studies provide other types of evidence that anadromous steelhead and resident rainbow trout forms can be derived from one another. Zimmerman and Reeves (2002) supplemented observations of temporal and spatial partitioning of spawning activity by rainbow trout and steelhead in the Deschutes River, Oregon, with analysis of strontium–calcium ratios in otolith nuclei that allowed maternal parentage to be determined. They found that all steelhead had steelhead mothers, and all resident rainbow trout had resident mothers, and concluded that the two life history forms functioned as separate biological species. However, in the Babine River, British Columbia, that

Zimmerman and Reeves (2002) also studied, 1 of 24 steelhead had a rainbow trout mother and two of nine resident rainbow trout had steelhead mothers. Using the same otolith analysis, Zimmerman et al. (2009) reported that presumptive steelhead smolts from the San Joaquin River, California, were derived from fish of both steelhead and rainbow trout maternal origin. Thrower et al. (2004b) crossed wild steelhead with resident, lake-dwelling rainbow trout originally derived from the same anadromous stock 70 years earlier and studied growth and life history transitions of progeny within and between lines. The lake population was isolated above waterfalls that prevented upstream migration, and thus there was strong selection against smolting in this population. Yet all crossings produced significant numbers of age-2 smolts, even in progeny of lake × lake pairs. Thrower et al. (2004b) suggested that the genetic potential for smolting can lie dormant or be maintained through a dynamic interaction between smolting and early maturation for decades even in the presence of selection against a migratory phenotype.

In this study we used a behavioral approach, and asked whether resident rainbow trout isolated above a waterfall that prevented upstream migration were able to express an anadromous life history form when experimentally transplanted to a downstream reach that had access to the ocean. To our knowledge, this experiment has not been previously undertaken.

The ability of resident rainbow trout to give rise to anadromous forms has important implications for management of steelhead, which have undergone precipitous declines in large portions of its native range. The National Marine Fisheries Service ruled that distinct population segments (DPSs) of steelhead subject to protection under the U.S. Endangered Species Act would be considered separately from resident rainbow trout (NMFS 2005), based on distinct physical, physiological, ecological, and behavioral differences between anadromous and resident forms. Busby et al. (1996) acknowledged that resident trout inhabiting areas upstream from barriers may contain genetic resources similar to those of anadromous fish within a basin or an evolutionary significant unit (ESU), but they concluded that little information is available on these fish or the role they may play in conserving natural populations of steelhead. If resident forms contribute to populations of anadromous adults, they could play a potential role in re-establishing or maintaining depressed or extirpated steelhead populations (Good et al. 2005).

The objective of the study was to compare movement and smolting status of resident rainbow trout that were isolated above an anadromous barrier in a coastal northern California stream with those of above-barrier trout that were experimentally relocated to a reach below the barrier in the same stream.

STUDY SITE

This study was conducted in Freshwater Creek, a fourth-order coastal stream in northern California (Figure 1). Freshwater Creek was selected for study for several reasons. It offers a barrier to upstream steelhead migration in the form of a

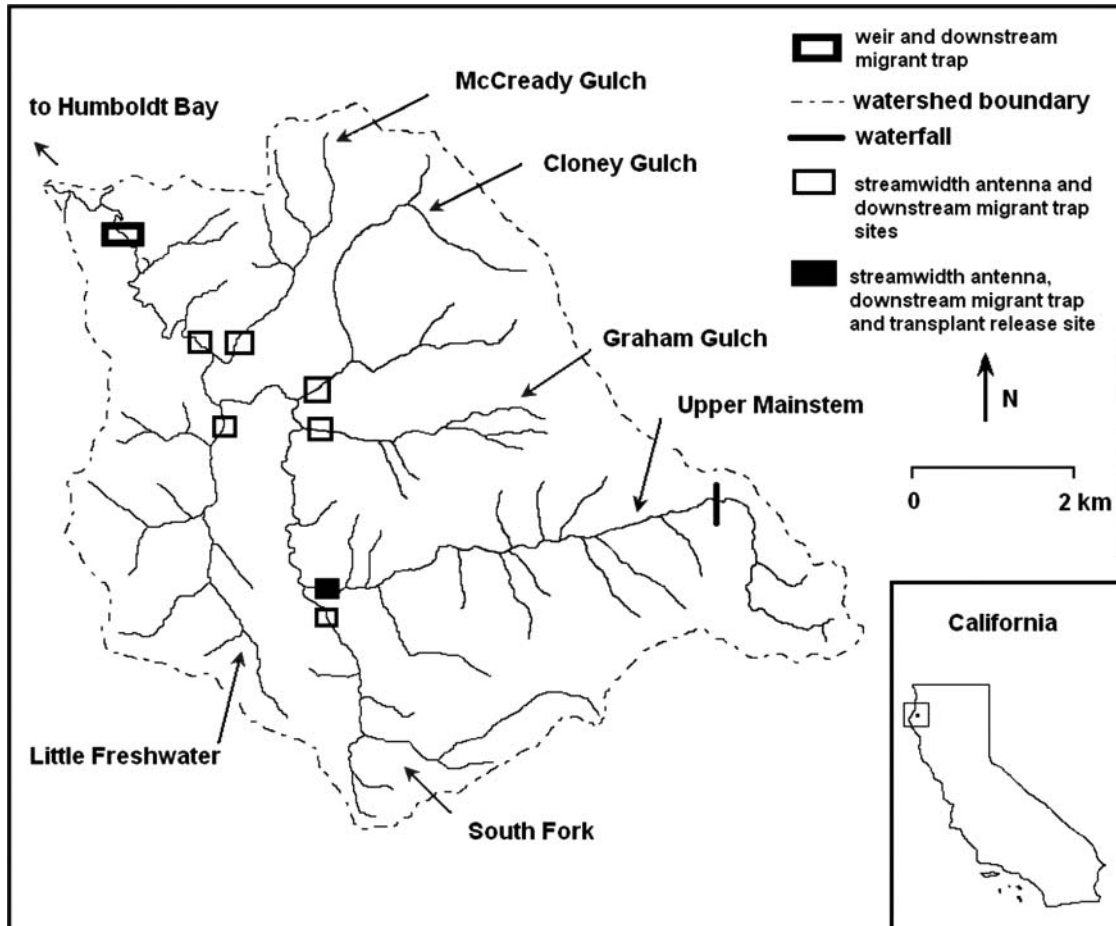


FIGURE 1. Location of Freshwater Creek in northern California (inset) and a watershed map showing the locations of the anadromous barrier waterfall and release point for transplanted rainbow trout, as well as locations of fixed antennae, downstream migrant traps, and the weir used to detect or capture transplanted trout.

waterfall on its upper main stem, and a small population of resident rainbow trout reside above the barrier. The origin and history of the above-barrier population are not known, but there are no records of stocking. Steelhead escapement is tracked by a nonprofit group at a permanent weir. Finally, during the period of this study, the California Department of Fish and Game (CDFG) monitored abundance and distribution of salmonid species occurring within the Freshwater Creek basin. This monitoring effort, which included use of smolt traps and stationary and portable antenna systems for detecting fish tagged with passive integrated transponder (PIT) tags within all major tributaries and in the main stem, as well as electrofishing and snorkeling surveys, increased the probability of detecting tagged rainbow trout that were transplanted below the barrier.

Freshwater Creek empties into Humboldt Bay and the Pacific Ocean after flowing through 7.1 km of the diked estuarine channels of Freshwater and Eureka sloughs. The watershed is 67.3 km² in area, 75% of which is managed for industrial timber production from upslope forests of coastal redwood *Sequoia*

sempervirens and Douglas fir *Pseudotsuga menziesii*. The main stem and five major tributaries provide approximately 30 km of habitat for anadromous salmonids. The upstream limit to anadromous migration on the main stem occurs at the base of a waterfall (40°44' 18.27" N, 124°00' 04.47" W) that is approximately 16 km upstream from the mouth of the creek where it enters estuarine slough. The vertical fall is 5 m high at summer base flow; step-pools that might allow for fish passage are not present. Several smaller waterfalls lie upstream from this barrier. Gradient of the above-barrier reach is steep. Approximately 1 km of stream provided available habitat, which consisted of a series of small step-pools within a confined channel. Land upstream from the waterfalls is undeveloped and without public access. Along with coastal rainbow trout and steelhead, the salmonid assemblage in Freshwater Creek includes Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and coastal cutthroat trout *O. clarkii clarkii*, as well as hybrids of rainbow trout and cutthroat trout (Voight et al. 2008). Other fishes present include prickly sculpin *Cottus asper*, coast range sculpin *C. aleuticus*, Pacific lamprey *Entosphenus tridentatus*,

brook lamprey *Lampetra pacifica*, and threespine stickleback *Gasterosteus aculeatus*.

Our experiment was conducted from October 2005 to October 2007. During the period of study, main-stem flows averaged 0.7 m³/s during summer months and were highly variable in winter. A peak discharge of 16.0 m³/s occurred in December 2005. Based on prorating flow from an adjacent watershed with a 30-year record (Bigelow 2003), the exceedance probability for this event was 2%. Climate in the region is characterized as marine west coast. Annual average precipitation is 100–200 cm, of which approximately 75% falls as rain between November and March. Average annual stream temperature was 11.0°C (range, 2.9–19.2°C).

METHODS

Transplantation experiment.—Above-barrier fish were sampled by electrofishing during three sampling events in 2005 and 2006 (October 2005, July 2006, and October 2006) to obtain a total of 131 individuals that were greater than or equal to 100 mm fork length (FL). Captured fish were anesthetized with a solution of tricaine methanesulfonate (MS-222) and individually implanted with a 23-mm, half-duplex PIT tag (Biomark). Coding of tag numbers was coordinated with the on-going CDFG program to ensure that duplicate tag numbers were not assigned. Individuals were weighed to the nearest 0.01 g and measured to the nearest 1 mm, and scale and fin samples were collected for age determination and genetic analysis, respectively. Tagged fish were allowed to recover in a bucket containing aerated water for approximately 10 min or until recovery was complete. Five above-barrier individuals were sacrificed for otolith extraction to evaluate maternal parentage.

One-half of the set of tagged individuals during any sampling event was released at the location of capture (total $n = 66$). The other half of the sample of tagged individuals was transported in a 19-L (5-gal) bucket containing aerated water to a release location approximately 5 km downstream from the waterfall (total $n = 65$), close to road access. Individuals were randomly assigned to an above- or below-waterfall release location. Transplanted fish were released in the main stem within a 100-m reach upstream from the South Fork confluence (Figure 1). From this location fish had unobstructed access to Humboldt Bay and the Pacific Ocean.

Several methods were used to relocate and recapture transplanted individuals. Tagged fish transplanted below the waterfall were detected (but not captured) with portable PIT tag interrogation systems as they moved through stationary stream-width antennae systems. Interrogation systems recorded the PIT tag number of the fish as well as the time of detection. Tagged fish were also captured in downstream migrant traps and during juvenile abundance and biannual night-dive surveys. Tagged fish above the barrier were recaptured during electrofishing operations in the fall of 2006 and 2007.

Stationary antennae were located in the lower main stem near Howard Heights Road in the town of Freshwater, in the upper main stem just upstream from the South Fork confluence (the farthest upstream major tributary confluence), and in the tributary mouths of South Fork, Cloney Gulch, Graham Gulch, and McCready Gulch, immediately upstream from their confluence with the main stem (Figure 1). The upstream extent of the stream–estuary ecotone (Miller and Sadro 2003) is at the lower main-stem site, 13 km upstream from Humboldt Bay; all antennae upstream from the lower main-stem site are within freshwater at all times. An antenna consisted of a single loop of braided copper electrical wire formed into a rectangle; the bottom of the rectangle was buried in the substrate and the top of the rectangle was positioned above the surface of the stream. Size of the antenna varied with stream width, and ranged from 1.3 × 3.8 m to 1 × 9.75 m. Two antennae were located at each site, approximately 2 m apart, to allow direction of tagged fish to be determined and to enable capture efficiency to be evaluated. Antennae detected the presence of 23- or 32-mm PIT tags. Detection data were recorded onto a battery-powered data logger circuit board (Oregon RFID, Portland) and records were uploaded weekly to a personal digital assistant (PDA; Palm Pilot M130). The antennae were operated year-round during this study except during high-flow storm events. When in operation, antenna detection rate was close to 100%.

The mobile PIT tag reader was a battery-powered backpack unit, which resembled a battery-powered backpack electrofisher, and included a wand. The same hardware used for the stationary antennae was fit onto a backpack frame and enclosed within waterproof housing. The antenna ran from the backpack through a 2-m length of polyvinyl chloride (PVC) tube and ended in a 61-cm-diameter circular antenna. The PIT tags could be read within approximately 1 m of the end of the wand, and individual tag numbers and a time stamps, as well as locations, were recorded directly onto a PDA M130. The mobile PIT tag reader was used during coordinated watershed surveys during May–June and again in October during both years of the study.

Tagged fish were also detected in downstream migrant traps. Downstream migrant traps were operated by the CDFG Anadromous Fish Research and Monitoring Program throughout the basin from March through June of each year, in locations immediately upstream from stationary antennae. Pipe traps were deployed in each of the five major tributaries as well as on the upper main stem, while a floating, inclined-plane trap was deployed at the lower main stem. In addition to these seven traps, a pipe trap for capturing outgoing salmonid smolts was also operated at the weir, 4.5 km below the lower main-stem site (Howard Heights) in the upper estuarine slough (Wallace 2003). Fish captured in migrant traps were scanned for the presence of PIT tags. Tagged fish were measured (± 1 mm FL), weighed (± 0.1 g), and classified as smolt, transitional, or resident based on visual examination of body morphology, spotting, coloration, and skin silvering (Viola and Schuck 1995). Smolts were distinguished by total silvering of the body and absence

of parr marks, fusiform body shape, blackening of the caudal fin tips, and light-colored bellies (Chrisp and Bjornn 1978). Transitional fish exhibited partial silvering of the body and fading but still had visible parr marks. Location of capture and PIT tag number were recorded. Individuals were assigned to age-classes based on length frequency analysis for Freshwater Creek steelhead conducted by CDFG (Ricker 2006). After they were processed, fish were released downstream from the trap.

Basin-wide summer juvenile abundance surveys conducted by the CDFG provided another opportunity for recapture of tagged fish. Surveys were conducted from 1 August to 1 October in 2005, 2006, and 2007 with a modified Hankin and Reeves (1988) protocol employing dive counts calibrated with electrofishing. Fish captured by electrofishing were scanned for the presence of tags. Recaptured fish were measured and weighed, and the location of recapture recorded. Finally, fish were recaptured during biannual night dives conducted by CDFG. Night dives were conducted in pool habitats on the upper main stem and South Fork of Freshwater Creek from 10 June to 10 July in 2005, from 10 June to 1 July in 2006, and from 1 October to 1 November in 2006. During these night dives, fish that were immobilized when suddenly exposed to the beam of a flashlight were captured with a dip net. Individuals were measured, weighed, and scanned for the presence of a PIT tag.

Otolith microchemistry.—Otolith samples collected from five above-barrier trout were analyzed for strontium: calcium (Sr:Ca) ratios in the otolith primordial and freshwater growth regions to evaluate an assumption that the population was derived from resident maternal parents. The ability of this analysis to distinguish resident from anadromous maternal parentage is based on (1) the substitution of strontium for calcium in the calcium carbonate matrix of the otolith at levels relative to the Sr:Ca ratio in the environment, (2) higher Sr:Ca ratios in seawater than in freshwater, and (3) yolk precursors, the composition of which is reflected in otolith primordium, develop in the ocean for anadromous forms (Zimmerman and Reeves 2002). Otoliths were cleaned and prepared by following the methods in Wells et al. (2003), and Sr:Ca ratios were analyzed by the U.S. Geological Survey, Alaska Science Center. Ratios were measured at 10 points each within the primordial and freshwater growth regions, and compared with paired with one-tailed *t*-tests with $\alpha = 0.05$. A higher Sr:Ca ratio in the primordial compared with the freshwater growth region of an otolith suggests an anadromous origin of the maternal parent, while the lack of a difference between the two regions suggests a resident origin.

Genetic analysis.—Because cutthroat trout and rainbow trout \times cutthroat trout hybrids occur within the basin, and field identification can be inaccurate (Voight et al. 2008), we undertook genetic analyses to ascertain the species identity of above-barrier individuals. Fin clips from 18 above-barrier trout were analyzed to determine probable genotypes by using restriction fragment length polymorphism (RFLP) procedures that used methods modified from Baumsteiger et al. (2005). Nuclear and mitochondrial markers that were fixed for alternate alleles

in coastal cutthroat trout and rainbow trout were chosen for analysis. In addition to the eight markers (seven nuclear DNA and one mitochondrial DNA) used by Baumsteiger et al. (2005), we also analyzed the loci *Occ-42*, *OM-47*, *Occ-35*, and *Occ-38* with forward and reverse primers (Ostberg and Rodriguez 2002). Genetic analyses were conducted in the Genetics Laboratory at Humboldt State University.

Growth analysis.—Length–mass relationships of *O. mykiss* between the above- and below-barrier reach were compared by covariance analysis to assess whether resident rainbow trout (above-barrier) and presumptive steelhead (below-barrier) differed in growth. Because many of the trout scales lacked a detectable first-year annulus, we were unable to compare growth through analysis of fish length or mass at age. Transplanted trout were excluded from the length–mass data set because they might not have experienced the same growth opportunities as did previous occupants of the below-barrier reach. Smolts and transitional individuals were also excluded from the data set because of the altered shape they assumed in preparation for marine life (Winans and Nishioka 1987). Length–mass relationships were compared for each of the 2 years of the study.

Movement analysis.—We graphically examined direction and distance traveled by transplanted rainbow trout and compared distance traveled between transplanted individuals and below-barrier residents. Distance was computed as the distance from the location of release (for transplanted individuals) or tagging (for below-barrier residents) to the location of last detection. Individuals greater than 100 mm FL tagged during fall night-dive surveys in the below-barrier population within 100 m downstream and 3,200 m upstream from the transplant location were used for movement comparisons. Individuals tagged during night-dive surveys were used in this analysis, rather than individuals captured in downstream migrant traps, because of their indeterminate life histories and proximity in size to the transplant group. Movement was determined with a combination of detections from stationary and mobile antennae, along with captures in downstream migrant traps. In a few instances, moribund individuals were detected, and these were determined to have moved only to the point of their last live capture.

RESULTS

Above-Barrier Population

All fish captured above the waterfall were identified in the field as rainbow trout. Although the population was not sampled with an objective of characterizing population structure, we observed that subyearling fish were sparse and that the population was dominated by yearling and older fish (Figure 2). Typically only 1–3 trout inhabited a pool, and many of the pools without trout were occupied by large (>200 mm) Pacific giant salamanders *Dicamptodon tenebrosus*. Individual trout selected for release below the waterfall ranged from 100 to 226 mm FL.

The age and size structure of the above-barrier population differed considerably from that of the below-barrier

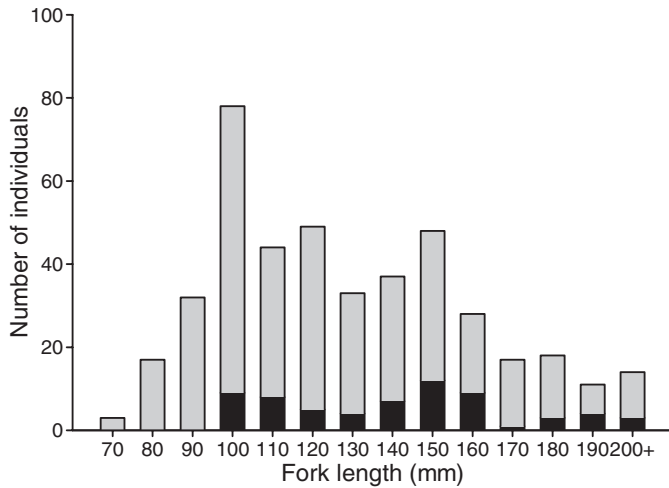


FIGURE 2. Fork length at capture of above-barrier rainbow trout in Freshwater Creek, categorized into 10-mm bins. Transplanted individuals are represented as black bars, and total numbers of individuals captured (excluding transplanted individuals) are represented as gray bars.

population into which they were transplanted (Figure 3). While the above-barrier population consisted primarily of yearling and older resident trout, the below-barrier assemblage was more numerous and dominated by age-0 progeny of anadromous *O. mykiss* in assemblages that also included juvenile coho salmon and cutthroat trout.

Otolith microchemistry from a small sample of above-barrier trout supported our assumption that these trout were progeny of resident rather than anadromous (maternal) parents. Differences in Sr:Ca ratios were not detectable between primordial and freshwater growth regions of the five otoliths that were examined (one-tailed *t*-tests: *df* = 9, all *P* > 0.05; Table 1).

Individuals genotyped from a sample of the above-barrier population all had some coastal cutthroat trout alleles. These individuals appeared to be backcross hybrids with rainbow trout (Figure 4). This population structure is indicative of a hybrid swarm consisting of an initial population with a higher proportion of rainbow trout individuals. The mitochondrial *ND1* marker indicated that all of the genotyped individuals were progeny of rainbow trout females. Rainbow trout × cutthroat trout hybrids have also been found in below-barrier reaches of

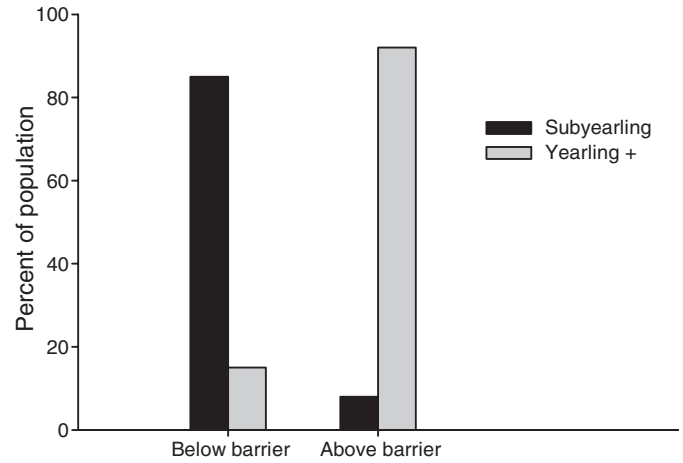


FIGURE 3. Age-class frequency of rainbow trout above the waterfall (*n* = 364) and below the waterfall (*n* = 1,300) in Freshwater Creek, California. Transplanted individuals are represented as black bars, and total numbers of individuals captured (excluding transplanted individuals) are represented as gray bars.

Freshwater Creek and in nearby streams; however, the majority of these showed preferential backcrossing with cutthroat trout rather than with rainbow trout (Baumsteiger et al. 2005).

Growth

Length–mass relationships did not differ between above- and below-barrier rainbow trout in Freshwater Creek in 2006 or 2007 ($F = 0.43$, $P = 0.51$ in 2006, and $F = 0.85$, $P = 0.36$ for 2006 and 2007; Figures 5, 6).

Movement

Movement of transplanted fish varied considerably among individuals (Figure 7). More than two-thirds (45 of 65) of the trout that were transplanted below the barrier to anadromy were resighted or recaptured during the 2-year study. Stationary antennae and portable PIT tag readers were similarly effective in detecting transplanted tagged fish, with the portable reader providing one or more detections of 30 individuals, and the stationary antennae providing one or more detections of 27 individuals. Downstream migrant traps captured seven tagged trout: five transplanted individuals and two individuals from the above-barrier release group. Tagged trout were not detected in

TABLE 1. Strontium: calcium ratios in the primordium and freshwater growth regions of the otoliths of five rainbow trout above the barrier in Freshwater Creek. The ratios were determined at 10 points in each of the two regions on each otolith; SDs are given in parentheses. The ratios were compared between the two regions with paired one-tailed *t*-tests; $P > 0.05$ indicates resident rather than anadromous maternal parentage.

Otolith	Primordium	Freshwater growth region	<i>P</i>
1	0.001257 (6.8×10^{-5})	0.00122 (8.8×10^{-5})	0.76
2	0.001099 (0.00011)	0.00096 (8.2×10^{-5})	0.98
3	0.001098 (7.8×10^{-5})	0.00106 (8.8×10^{-5})	0.67
4	0.001132 (8.7×10^{-5})	0.00125 (0.00013)	0.93
5	0.00127 (8.9×10^{-5})	0.00107 (3.4×10^{-5})	0.99

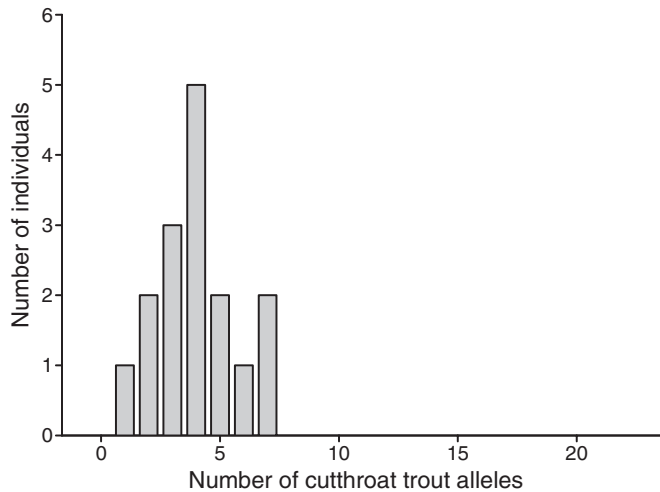


FIGURE 4. Frequency of cutthroat trout alleles in above-barrier trout ($n = 18$) at 11 loci that differentiate between rainbow trout and cutthroat trout. The presence of zero alleles suggests a pure strain coastal rainbow trout, 22 alleles suggest a pure strain coastal cutthroat trout, and 11 alleles indicate a putative F_1 hybrid.

summer juvenile abundance surveys or during fall and summer night dives. Most of the detected individuals ($n = 31$) remained within 500 m of the release location in all sightings. Upstream movement was observed in two individuals last detected within 300 m of the waterfall, approximately 4.5 km from the release location. Transplanted individuals were never detected above the waterfall after downstream release. Six transplants traveled in a downstream direction but still remained in freshwater. Of these, only one entered and remained in a tributary. In a 5-d period, a single individual traveled over 6 km downstream, entering three separate tributaries before returning to the main stem, where-

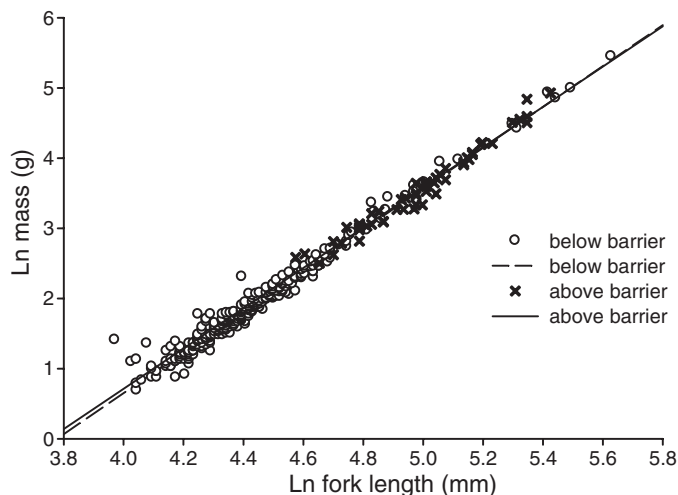


FIGURE 5. Length-mass relationships of above-barrier ($n = 57$, $R^2 = 0.97$) and below-barrier ($n = 313$, $R^2 = 0.97$) rainbow trout in Freshwater Creek, California, in 2006. Differences between populations in slopes and intercepts of regression lines were not significant ($F = 0.43$, $P = 0.51$).

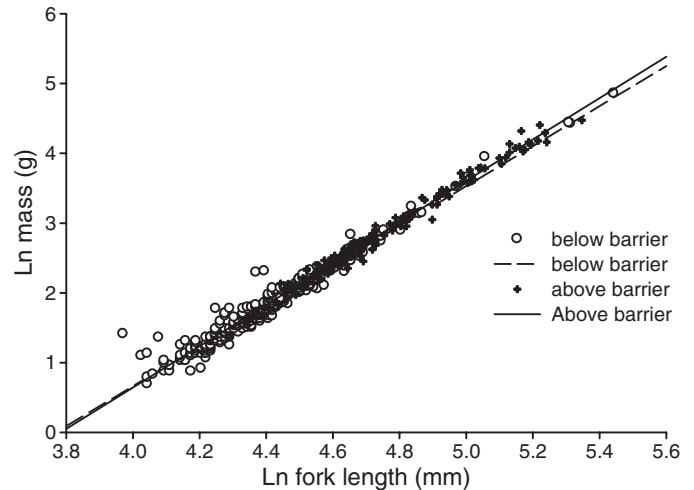


FIGURE 6. Length-mass relationships of above-barrier and below-barrier rainbow trout in Freshwater Creek, California, in 2007. Differences between populations in slopes and intercepts of regression lines were not significant ($F = 0.85$, $P = 0.36$).

upon it entered tidally influenced water and returned within hours to the nontidal main stem. Two transplanted individuals were last detected in tidally influenced waters. Both detections in tidal water occurred in late November, within approximately 4 months of their release below the waterfall.

Approximately one-quarter (15 of 66) of the tagged trout released above the barrier were recaptured above the barrier, and three individuals were found alive below the barrier in Freshwater Creek. Two tags from moribund individuals that were released above the waterfall were also discovered near the base of the waterfall and originated from individuals initially captured

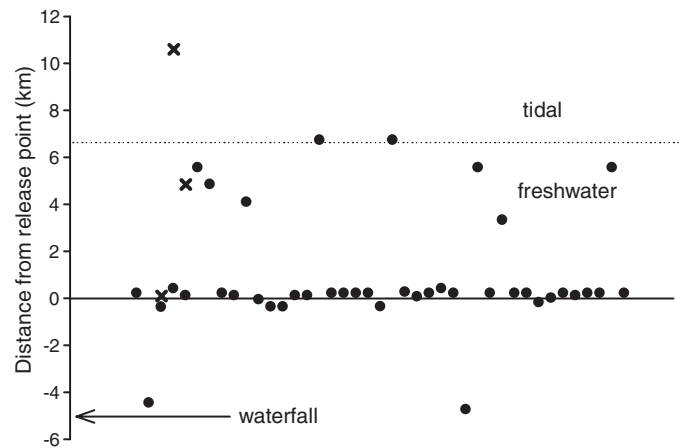


FIGURE 7. Distance traveled (km) by tagged trout from the release point below the waterfall to the last location in Freshwater Creek where the trout were known to be alive. Negative numbers represent upstream movement, and positive numbers represent downstream movement. Each filled circle represents one transplanted trout ($n = 41$), and x symbols represent tagged trout released above the barrier ($n = 3$). The upstream limit of tidal influence occurs at 6.5 km; the waterfall is at -5 km.

TABLE 2. Numbers of tagged rainbow trout from the above- and below-barrier release groups found in different sections of Freshwater Creek at last sighting or recapture. The above-barrier trout were released in a reach no more than 1 km upstream from an impassable waterfall; the below-barrier trout were released approximately 5 km downstream from the waterfall. Within the below-barrier group that was last located in the vicinity of the release site, one fish had smolted and one was a presmolt. One fish released above the barrier and last located in the upper estuarine slough had also smolted.

Rainbow trout released and later detected	Above-barrier release	Below-barrier release
Number released	66	65
Number resighted	20	45
Location at last detection		
Above waterfall	15	0
Base of waterfall \pm 300 m	2	2
Transplant release site \pm 500 m	1	34
Below release site, freshwater	1	7
Below release site, tidal	1	2

from a reach within 1,000 m of the waterfall. Moribund individuals were discovered during surveys with portable PIT tag readers, and their date of death was not known. However, mortality was not likely to have been associated with tagging or handling, as the surveys occurred 6 months or more after the timing of initial capture and release. Of the three trout released above the barrier that were located downstream from the waterfall, two were in freshwater, approximately 5 and 10 km downstream from the waterfall, and one was found in tidal water (Figure 7; Table 2).

Capture of trout in downstream migrant traps allowed us to assess smolting status. Two of seven tagged trout captured in the traps had smolted, and one was judged to be a presmolt. The presmolt was a transplanted fish. One of the smolts was also a transplanted individual, and one was from the above-barrier release group. At release, the transplanted fish measured 185 mm FL and weighed 82 g. On recapture in late April 6 months later, the fish increased 7 mm in length and lost 12 g. The smolt from the above-barrier release group was captured in early May, 18 months after its release, in the farthest downstream trap (weir trap) in the upper estuarine slough. All of the fish transplanted downstream were captured in the farthest upstream trap (closest to the release location).

While only a small percentage of transplanted trout (2%, i.e., 2 of 65 transplants) were last detected in tidally influenced water, the percentage of below-barrier trout that were initially captured and tagged in the vicinity of the transplant release location and later captured in tidally influenced water was also small. Of 210 previous downstream inhabitants that were greater than 100 mm FL, 4% ($n = 9$) were subsequently captured in tidally influenced water during the course of this study.

DISCUSSION

Movement patterns displayed by the transplanted fish in our study may have been biased by the act of transplantation, as the fish were introduced into downstream habitat already colonized with prior occupants. Above-barrier residents enjoyed lower than equilibrium density after the removal of transplants. A reciprocal transplant of below-barrier individuals into above-barrier habitat would have completed the experimental design and strengthened the study, but we did not receive permission to undertake the reciprocal transplantation. Food resources were likely to have been lower above than below the falls, but the similarity of the length–mass relationship of above- and below-barrier trout suggests that the fish in both habitats were growing at the same rate. In contrast to findings of Letcher et al. (2007) that brook trout *Salvelinus fontinalis* isolated above barriers exhibited low early juvenile mortality, and an age distribution skewed toward younger, smaller fish, we observed an above-barrier age distribution skewed toward larger size-classes. The apparent high early juvenile mortality of trout above the falls may have reflected a paucity of refuges from larger fish and other predators in small step-pool habitat.

Detection of a few, but not many, above-barrier individuals below the waterfall raises an interesting question about whether above-barrier fish engage in an active effort to stay above the falls. Eight of the fish released below the falls traveled over 3 km downstream. Above-barrier fish were captured and released within 1 km of the falls. If trout movement is similar above and below the barrier, a greater number of above-barrier individuals would be expected below the falls. That we failed to detect more fish suggests that when above-barrier fish encountered the barrier, they chose to stay above it. The mechanism by which this might occur is unknown. Our finding of two dead above-barrier trout at the base of the falls suggests that not all individuals may be successful in the endeavor.

We have no direct evidence that any transplanted fish went out to sea. Adult returns of fish transplanted in 2005 and 2006 were not observed at the weir in 2007 or 2008, and given the very low survivorship that characterizes salmonid populations in marine environments (Quinn 2005) it would be remarkable to observe any adult returns of these transplanted trout. The individuals that were last detected moving downstream in the lower main stem of the river were in or close to a saltwater transition area and may have been traveling to the estuary or sea, but this is only supposition. Morphological changes associated with smolting were found in only one transplanted trout, with another fish identified as transitional. Nonetheless, evidence of smolting in just these few individuals demonstrates the potential for resident rainbow trout to express migratory behavior and to enter breeding populations of steelhead. Thrower et al. (2004b) also demonstrated that smolting can arise in the progeny of resident \times resident rainbow trout matings.

Detection of tagged trout below the waterfall that were released above the waterfall also suggests the possibility of gene

flow from above to below barriers. This is reinforced with the finding that a rainbow trout released above the waterfall and later detected below the barrier was also smolting. Pearse et al. (2009) also found that resident rainbow trout above a waterfall in a coastal California stream occasionally descended over the falls, but genetic data suggested that they remain differentiated from below-barrier steelhead. Gene flow may occur, however, even in the presence of substantial differences in microsatellite allele distributions. Levels of gene flow are also likely to be site-specific. In comparing the genetic structure of above- and below-barrier rainbow trout populations within the nearby Russian River basin, Deiner et al. (2007) found that specific above-barrier sites had populations that were genetically distinct from those that had access to the ocean, while others sites did not. We abandoned planned genetic comparisons of above- and below-barrier rainbow trout populations after failing to identify pure strain rainbow trout above the waterfall. The effect of hybridization on the movement patterns that we observed in the transplanted trout is unknown.

The low incidence of smolting that we observed in the transplanted trout might have been affected by fish size. Many of the fish tagged above the falls were large and beyond the size threshold (140 mm FL) at which the parr-smolt differentiation commonly occurs (Peven et al. 1994). Transplantation of smaller individuals might have resulted in an increased occurrence of smolting and migratory behavior. In our study, the lengths of (192 and 203 mm FL) of the two tagged fish that did smolt were larger than the average length (156 mm) of steelhead smolts in the basin (Ricker 2003). Sexual maturation and smolting are presented as requiring mutually incompatible developmental conversions (Thorpe 1986, 1987), and generally trout that mature sexually as parr do not smolt and go to sea (Nordeng 1983; Jonsson 1985; Jonsson and Jonsson 1993). However, Shapovalov and Taft (1954) reported evidence of *O. mykiss* maturing in freshwater and spawning before their first ocean migration. Busby et al. (1996) mentioned that this life history variant has also been described for cutthroat trout and some male Chinook salmon. Whether the two fish that smolted in this study had previously matured and spawned in freshwater is unknown, as scale analysis was inconclusive.

Our findings have conservation and management implications, which are complicated by issues of hybridization. Hybridization between rainbow trout and coastal cutthroat trout is commonplace along the coast of western North America, even in locations that are believed to be pristine (Young et al. 2001; Williams et al. 2007). Concerned that hybridization may compromise recovery of declining native trout populations through disruption or loss of native genomes, Allendorf et al. (2001) proposed guidelines for managing hybridized populations. Peacock and Kirchoff (2004) and Williams et al. (2007) countered that their inflexible application could unnecessarily compromise the evolutionary potential of a species (Peacock and Kirchoff 2004; Williams et al. 2007), and argued that policies for dealing with salmonid hybrids should be context-specific.

Hybridization issues aside, the emigration of above-barrier resident trout to downstream reaches that we observed, evidence that resident trout can transform directly into smolts, and similarity in movement between transplanted trout and previous inhabitants of downstream reaches, together suggest that exclusion of resident rainbow trout from protection and recovery efforts afforded to steelhead would clearly be misguided, at least in this northern California basin. The extent to which steelhead and resident rainbow trout interchange life history forms within a basin, and the conditions giving rise to the interchange, warrant further examination.

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