Comparisons between hatchery and wild steelhead trout (*Oncorhynchus mykiss*) smolts: physiology and habitat use

Megan S. Hill, Gayle Barbin Zydlewski, and William L. Gale

Abstract: Hatchery steelhead trout (*Oncorhynchus mykiss*) smolts, progeny of a newly founded native origin broodstock, were released into Abernathy Creek, Washington, in 2003 and 2004. After release, saltwater tolerance, gill Na^+,K^+-ATPase activity, and habitat use were compared. A subsample of hatchery and wild steelhead trout were implanted with 23 mm passive integrated transponder (PIT) tags each year. PIT-tagged migrants were used for physiological comparisons. Hatchery fish were significantly larger than wild fish. Hatchery migrants expressed significantly lower levels of gill Na^+,K^+-ATPase activity than wild migrants. After a 24 h seawater challenge, hatchery migrants had significantly higher plasma osmolality and [Na^+] than wild migrants. Microhabitat use of PIT-tagged hatchery and wild individuals in a control (wild fish only) and effect (hatchery and wild fish) site were compared before and after the introduction of hatchery fish. No difference was detected in hatchery and wild smolt habitat use. Wild fish did not change their habitat use after the introduction of hatchery fish. Although hatchery and wild fish differed in smolt physiology, differences in short-term use of freshwater habitat were not detected, and hatchery fish did not appear to displace wild fish.

Résumé : Des saumoneaux de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*), issus d'une nouvelle souche reproductive indigène et élevés en pisciculture, ont été relâchés dans Abernathy Creek, Washington, en 2003 et 2004. Après la libération des poissons, nous avons comparé la tolérance à l'eau de mer, l'activité de la Na^+,K^+-ATPase des branchies et l'utilisation de l'habitat. Les deux années, nous avons implanté des étiquettes PIT (transpondeurs passifs intégrés) de 23 mm dans un sous-échantillon de truites arc-en-ciel de pisciculture et de truites sauvages. Les migrateurs munis de PIT nous ont permis de faire des comparaisons physiologiques. Les poissons de pisciculture sont significativement plus grands que les poissons sauvages. Les migrateurs de pisciculture exhibent des niveaux significativement plus bas d'activité de la Na^+,K^+-ATPase branchiale que les migrateurs sauvages. Après une exposition de 24 h à l'eau salée, les migrateurs de pisciculture ont une osmolalité plasmatique et une concentration de [Na^+] significativement plus élevées que les migrateurs sauvages. Nous avons comparé l'utilisation des microhabitats chez des poissons porteurs d'étiquettes PIT de pisciculture et d'origine sauvage dans des sites témoin (poissons sauvages seul) et expérimental (poissons d'élevage et d'origine sauvage) avant et après l'introduction des poissons de pisciculture. Il n'y a pas de différence d'utilisation de l'habitat entre les saumoneaux de pisciculture et les saumoneaux sauvages. Les poissons sauvages ne changent pas leur utilisation de l'habitat après l'introduction des poissons de pisciculture. Bien que la physiologie des saumoneaux soit différente chez les poissons de pisciculture et les poissons sauvages, nous ne détectons aucune différence à court terme de l'utilisation de l'habitat d'eau douce et les poissons d'élevage ne semblent pas déplacer les poissons sauvages.

[Traduit par la Rédaction]

Introduction

Hatchery smolts are increasingly being used to supplement wild populations of salmon and steelhead trout (*Oncorhynchus mykiss*) in the Pacific Northwest (Peery and Bjornn 2000). Most supplementation hatchery programs aim to minimize genetic and ecologic impacts on wild populations. The majority of work to date has examined genetic effects of hatcheries (Weber and Fausch 2003). Despite genetic similarity, in some instances juvenile hatchery fish differ physiologically, morphologically, and behaviorally from wild fish at release (reviewed by Weber and Fausch 2003). These biological differences can affect survival by contributing to individual fish interactions and interactions of fish with their

Received 23 September 2005. Accepted 6 March 2006. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 22 June 2006.
J18899

M.S. Hill,[1,2] G.B. Zydlewski,[3] and W.L. Gale. US Fish and Wildlife Service, Abernathy Fish Technology Center, 1440 Abernathy Creek Road, Longview, WA 98632, USA.

[1]Corresponding author (e-mail: mshill@uga.edu).
[2]Present address: Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA.
[3]Present address: University of Maine, School of Marine Sciences, 5741 Libby Hall, Orono, ME 04469-5741, USA.

 doi:10.1139/F06-061

environment. Key components of survival to adult return are adequate smolt development upon release (Zaugg 1989; Zaugg and Mahnken 1991; Beckman et al. 1999) and juvenile freshwater habitat use (Gatz et al. 1987).

Numerous studies have demonstrated that if hatchery releases are timed in concert with smolt development, survival and migration tendency are enhanced (Harache et al. 1980; Zaugg 1989; McCormick et al. 2003). Smolt development occurs in response to a combination of biotic and abiotic cues including temperature, photoperiod, and nutritional status (Grau et al. 1982; McCormick et al. 2000; Beckman et al. 2003). Often these factors differ greatly between the hatchery and wild environments.

Hatchery-reared fish released as smolts often differ in size and degree of smolt development from their wild (Leonard and McCormick 2001) or wild-reared counterparts (McCormick et al. 2003), despite their genetic similarity. In addition, genetically similar fish with differing rearing conditions have been shown to exhibit differing adult and parr phenotypes (Fleming et al. 1994; Kostow 2004) and behavior (Symons 1969; Kostow 2004) when released into the wild. These factors, as well as size (Spina 2003) and shape of fish (Bisson et al. 1988), all affect salmonid habitat use in the wild.

Water depth, velocity, substrate, and cover are critical to the distribution and abundance of juvenile salmonids (Armstrong et al. 2003). Laboratory studies show that domesticated hatchery and wild salmonids often use habitat characteristics differently (Mesa 1991; Berejikian 1994; Deverill et al. 1999). However, these studies were conducted on life stages other than smolts, and the use of these habitat characteristics changes throughout a fish's development. For this reason, the life stage at which fish are released will effect their habitat requirements and their interactions with wild fish. The majority of anadromous salmon and trout reared in the Pacific Northwest are currently released as smolts (National Marine Fisheries Service (NMFS) 2003). Despite the marked difference in physiology and behavior between the life stages and the dominance of smolt releases, there are few studies of hatchery and wild smolt interactions in the freshwater environment (for exception, see McMichael et al. 1999) and no known studies of steelhead trout smolt habitat use.

We used hatchery-reared and wild steelhead trout with the same genetic background to address several specific objectives. First, we compared the morphological and physiological characteristics of first-generation hatchery fish and their wild counterparts. Physiological changes are linked to behavioral changes (Zydlewski et al. 2005) and ultimately affect habitat use. Our second objective was to answer questions regarding hatchery and wild fish habitat use. (*i*) Of the randomly available habitat, what do hatchery and wild smolts use? (*ii*) Do hatchery and wild smolts use different habitats? (*iii*) Does the introduction of hatchery fish change the habitat use of wild fish?

Materials and methods

Study site

Abernathy Creek, a tributary to the Columbia River, in Longview, Washington, USA, is a small, third-order stream with a drainage area of approximately 110 km^2. It supports several native salmonids: steelhead trout, coho salmon (*O. kisutch*), cutthroat trout (*O. clarkii clarkii*), and chum salmon (*O. keta*) and an introduced run of fall Chinook salmon (*O. tshawytscha*).

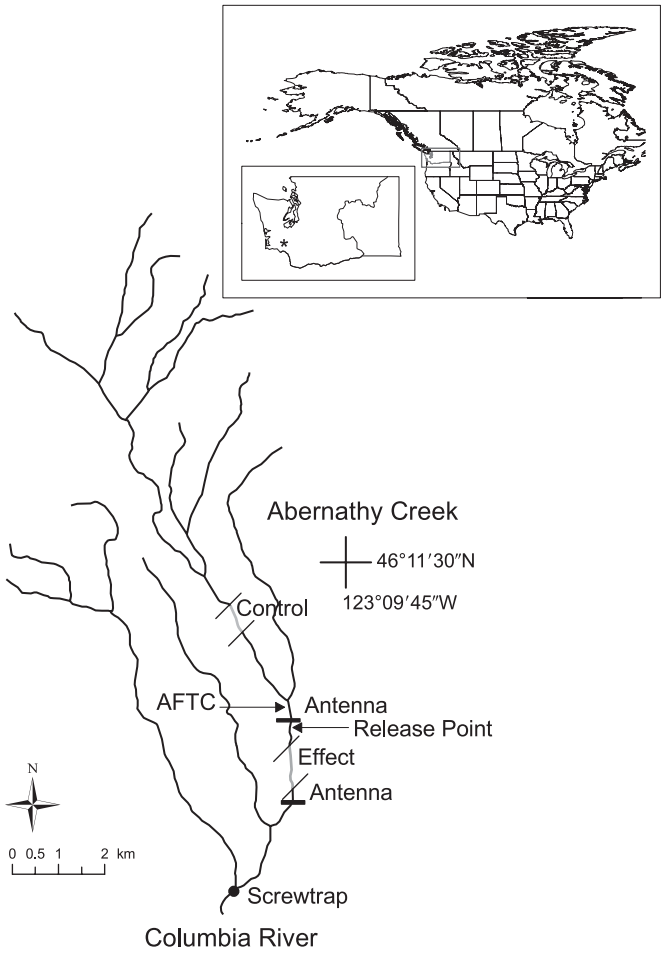


Fig. 1. Habitat assessments and wild steelhead trout (*Oncorhynchus mykiss*) collection occurred in Abernathy Creek, Longview, Washington (noted by an asterisk (*) on the inset map). Control and effect sites were identified in 2003, electrofished in 2003 and 2004, and assessed for habitat availability in both years (shaded lines indicate site boundaries). Two stationary portable integrated transponder (PIT) tag antenna arrays were located on either end of the effect site (solid black bars). A screw trap was operated at the mouth of Abernathy Creek.

In 2003, two sections of Abernathy Creek were designated as control (wild fish only) and effect (wild and hatchery fish) sites (Fig. 1). Hatchery fish were released from Abernathy Fish Technology Center (AFTC) at stream km 3.4. The effect site was located 0.5 km downstream of AFTC and the control site was located 3 km upstream of AFTC. No hatchery fish were released upstream of the control site. The effect site was 0.5 km long and the control site was 0.8 km long (11 m mean stream width).

Fish

Wild steelhead

In the control and effect sites, five-pass electrofishing (Zippin 1958) was conducted to estimate initial density of

Table 1. Number of PIT (passive integrated transponder) and CWT (coded wire) tagged hatchery steelhead trout (*Oncorhynchus mykiss*) released per raceway (RW) in 2003 and 2004.

	RW 3		RW 4		RW 5	
	PIT	CWT	PIT	CWT	PIT	CWT
2003						
Steelhead	321	10 130	348	10 058	331	10 886
Release date	17 Apr		1 May		16 May	
Total no. released	281	10 063	304	9854	288	10 796
2004						
Steelhead	457	9811	466	9711	469	10 522
Release date	14 Apr		28 Apr		15 May	
Total no. released	405	9741	431	9668	462	10 501

juvenile steelhead trout in 2002 (10 September and 25 October) and 2003 (30 September and 29 October).

In September of 2001, 2002, and 2003, as part of another study, we captured steelhead trout larger than 100 mm fork length (FL) by electrofishing (Smith Root LR-24; Smith Root Inc., Vancouver, Washington) in the 13 km of Abernathy Creek upstream of AFTC. All individuals were tagged with a 23 mm (23 mm long, 3.4 mm wide, and 0.6 g in air) passive integrated transponder (PIT) tag. Captured steelhead trout were anesthetized with clove oil (25 ppm) and a PIT tag was inserted into the fish via an incision into the peritoneal cavity (Zydlewski et al. 2003). Capture location (to the nearest 0.5 km), FL, weight, scale samples (for aging), and a left ventral fin clip (for genetics) were collected from all individuals that were tagged. In 2001, we tagged 1099 steelhead trout. In 2002, we tagged 1360 steelhead trout, 119 in the control site and 130 in the effect site. In 2003, 2708 steelhead were tagged, 185 in the control site and 111 in the effect site. Nonlethal gill samples for Na^+,K^+-ATPase activity were collected on a subset (n = 35 per year) of fish collected from the effect site. After recovery, fish were released back into Abernathy Creek near their capture location.

Hatchery steelhead

Hatchery fish were progeny of native Abernathy Creek broodstock. Five hundred parents had been removed by electrofishing the creek and collecting young-of-the-year (0+ year class) steelhead in September of 1999 and subsequently raising them in freshwater to sexual maturity at AFTC. In late winter and early spring of 2001, 120 pairs (240 fish) were spawned as 2-year-olds. Resulting families were culled to 1000 eyed eggs to minimize family size variance. This procedure for fish collection, rearing, and spawning was repeated for brood year (BY) 2000 except that each full-sib family was culled to 350 eyed eggs. Fish were reared at an average density of 278 fish·m^{-3} in three concrete raceways receiving a constant flow of creek water. Raceways were covered with bird netting and had partial overhead cover. Steelhead had continual access to demand feeders and were handfed daily. In April and May of 2003 (BY 1999) and 2004 (BY 2000), 30 000 age-1+ steelhead trout smolts were released into Abernathy Creek. In each release year, fish were released by raceway in three separate groups, and the release dates occurred at 2-week intervals starting in mid-April. In both years, the first release group consisted of progeny from early in the spawning season and the final release group was from late in the spawning season.

A subset of hatchery fish were PIT tagged in January 2003 (BY 1999, n = 957) and January 2004 (BY 2000, n = 1392) when they were 163 ± 40 mm (mean ± standard deviation) FL and weighed 43 ± 26 g (Table 1). Over a 3-day period, all fish were removed from a crowded section of a raceway to a trough for coded wire tagging. In 2003, approximately every 25th fish was given a 23 mm PIT tag rather than a coded wire tag. In 2004, all fish were coded wire tagged and adipose fin clipped, and approximately every 25th fish also received a PIT tag (Table 1). Fish were monitored for tag loss and mortality during the period between tagging and release.

A subset of fish was measured (FL and weight) and gill biopsies were removed in fall, winter, early spring, and the day before release in 2003 and 2004. On each of these dates, approximately 100 steelhead were dipnetted from each raceway; from this group, we randomly selected 20 fish for sampling (size measurements and a nonlethal gill sample). Gill Na^+,K^+-ATPase activity and size data were compared among sample dates and raceways using two-way analysis of variance (ANOVA; factors: raceway and sample date).

Body size and physiology

Washington Department of Fish and Wildlife (WDFW) operated a screw trap at the mouth of Abernathy Creek from early April to mid-June in 2003 and 2004. All PIT-tagged wild and hatchery steelhead trout caught at the trap were anesthetized with MS-222 (tricaine methane sulfonate, 98 mg·L^{-1}, buffered with sodium bicarbonate to pH = 7.0). We measured FL and weight and removed a nonlethal gill biopsy (McCormick 1993) from all PIT-tagged hatchery and wild steelhead trout captured. After recovery, fish were released downstream of the screw trap. Gill biopsies were collected into ice-cold SEI buffer (250 mmol·L^{-1} sucrose, 10 mmol·L^{-1} Na_2-EDTA, 50 mmol·L^{-1} imidazole, pH = 7.3), frozen on dry ice, and stored at –80 °C. Gill samples were assayed for Na^+,K^+-ATPase activity using the method of McCormick (1993).

In 2004, 3 days after each hatchery release, hatchery and wild fish (migrants) were captured at the screw trap, transferred to the laboratory (within 1 h of removal from the screw trap), and immediately exposed to seawater (32 ppt) for 24 h. The seawater challenge system consisted of duplicate circular tanks (1.2 m diameter; 710 L) connected to a chiller and pump used for recirculation. The chiller maintained water temperature between 11 °C and 14 °C. A total of three trials were conducted, each corresponding to a different hatch-

ery release group. Hatchery and wild fish were held together in the same tank during the seawater exposure, and fish from each group were split evenly between the duplicate tanks. After exposure, fish were killed using an overdose of MS-222, and blood was collected from the caudal vein using heparinized syringes. Gill samples were collected and assayed for Na^+,K^+-ATPase activity using the method of McCormick (1993). Plasma [Na^+] was determined using an electrolyte analyzer (AVL 984; AVL Medical Instruments, Roche Diagnostics, Branchburg, N.J.), and plasma osmolality was measured with an osmometer (Osmette II; Precision Systems, Natick, Mass.).

FL, condition factor, and gill Na^+,K^+-ATPase activity of fish passing through the screw trap were compared using two-way ANOVA. All data met the assumptions of ANOVA, with the exception of 2004 gill Na^+,K^+-ATPase data. The transformation of the 2004 gill Na^+,K^+-ATPase data that met the assumptions of equal variances but violated the assumption of normality was utilized as no transformation satisfied both assumptions (per Scheffe 1959). Differences between spawning time of adults and release dates could lead to differences in fish size and gill Na^+,K^+-ATPase activity. Therefore, date (within year) was treated as a factor in the two-way ANOVA, and three blocks of time were created to correspond with each release (Table 1). Wild fish were included in the block that encompassed the date when they passed through the screw trap. Rearing type (hatchery and wild) and date (three release blocks) were the factors in the ANOVA. Plasma [Na^+] and osmolality data were analyzed with two-way ANOVA using tank and rearing type as the factors for the ANOVA.

Habitat availability

To determine habitat types available to fish, we measured physical habitat characteristics at several stratified random points throughout the control and effect sites on 28 May 2003 and 29 May 2004. Transects were positioned two mean stream widths (MSW) apart throughout the site to ensure that all habitat types were encountered (Simonson et al. 1994). In 2003, we collected habitat availability data by selecting one random location along each transect (25 transects were available per site). In 2004, we expanded the data collection method to record habitat availability throughout the season. Ten random transects were selected on each survey date and habitat measurements were recorded at one random location (randomly selected distance from the left stream bank) on each transect.

Water depth was measured to the nearest 0.1 dm. Velocity ($m \cdot s^{-1}$) was measured at 0.60 of the known water depth using an automated flow meter (model 1215; Scientific Instruments Inc., Milwaukee, Wis.). We classified the dominant substrate size at each fish detection site according to the modified Wentworth scale (Bain and Stevenson 1999). Cover was ranked on a scale of 1 to 16 according to Baltz et al. (1991). This ranking considered all possible combinations of surface turbulence, objects (i.e., debris and boulders of various size classes), rootwads, undercut banks, and overhanging vegetation. Shading was measured in µmoles using an automated light meter (model LI-250; LI-COR Inc., Lincoln, Nebraska). The light meter was positioned directly over the fish detection site (in air) so that we avoided shadowing the meter. In 2004, we recorded light readings directly above the water surface as in 2003 and at the same depth as flow measurements, 0.60 of the water depth. We categorized habitat as riffle, run, glide, or pool as described by Bain and Stevenson (1999).

To detect differences in habitat availability between the years, random habitat measurements on 28 May 2003 were compared with measurements from 29 May 2004. The two factors were year (2003 and 2004) and site (control and effect). After transformation, all data were normally distributed with equal variances.

Habitat use

In 2003 and 2004, 2 weeks before hatchery release, PITpacks (Hill et al. 2006) were used to monitor wild steelhead trout habitat use in the control and effect sites of Abernathy Creek. PITpacks are portable PIT tag detection devices that are used to scan wadeable streams in search of fish. When a tagged fish approaches the PITpack antenna or the antenna approaches a tag (within 90 cm), the PITpack beeps and records the individual PIT code. We routinely and systematically scanned the control and effect sites with PITpacks (twice before each hatchery release and twice after each release).

On each survey day, at the downstream boundary of the site, antennas of the PITpacks were submerged in the creek and tuned to the daily water conditions. Two PITpack operators then slowly moved upstream through the site scanning all available habitats. The antenna was held at a 45° angle perpendicular to water flow whenever feasible. The two operators worked through the sites, walking side-by-side, each scanning half of the creek. Fish location was considered the spot with the highest frequency of tag readings (indicated by the beeper). When a tagged fish was detected with a PITpack, we recorded the individual tag code and marked the detection site with GPS (global positioning system) and flagging. Habitat use data were collected at fish detection locations as indicated by flagging and GPS coordinates. In 2003, habitat characteristics (water depth, velocity, substrate, cover, shading) were recorded by a third observer immediately after detection. In 2004, the two PITpack operators returned at the end of the day to record habitat measurements at all detection and random sites.

To quantitatively describe hatchery and wild habitat use, we compared randomly chosen habitat availability measurements taken throughout the season in 2004 with measurements taken at detection locations of hatchery and wild steelhead trout in 2004 using one-way ANOVA (factor: detection location) with pairwise comparisons for all habitat characteristics. We transformed data to meet the assumptions of equality of variance and normality. The use of habitat types (riffle, run, glide, pool) by hatchery and wild fish were also compared using chi-square analysis. We tabulated the number of riffles, runs, glides, and pools available, as well as the number of fish detected in each of these habitats.

To determine if hatchery and wild fish differed in their habitat use, we analyzed 2003 and 2004 data using a nested ANOVA. Habitat characteristics at the position of fish detection were transformed to meet the assumption of equality of variances and normality whenever possible. In instances when normality could not be satisfied (substrate and cover), the transformation of raw data that satisfied the assumption of

equality of variances was used (per Scheffe 1959). Rearing type was the fixed factor in the model and year was the random factor. Analyses that did not have a significant random effect (year) were pooled and the years were analyzed collectively (depth, velocity, and substrate). In addition, we used nonmetric multidimensional scaling ordination (MDS) to examine the habitat characteristics collectively, $\log(x + 1)$-transformed data were used because of the exponential scale of the light measurements. We used MDS rather than principle components analysis (PCA) because of the small sample sizes and nonlinearity of the data.

To detect differences in habitat use of wild fish after the release of hatchery fish, we used a before–after, control–impact (BACI) procedure. Control and impact (effect) sample data were separated into before (the first release) and after (the first release) groups by week and compared using two-way ANOVA (as described by Underwood 1992). Fixed factors included before–after groups (BA), control–impact sites (CI), and BA·CI. We treated survey week as a random, repeated measure because of the potential lack of independence between surveys. A significant BA effect indicated that fish habitat use of the two sites differed significantly during the two survey periods. A significant CI effect indicated that the use of habitat by fish differed between the sites. A significant interaction indicated that fish habitat use in the two sites was different after the release.

Fish emigration

Hatchery and wild fish were also detected moving out of the control and effect sites using stationary PIT tag interrogation systems already established on Abernathy Creek (Zydlewski et al. 2003). Systems were designed to report all detected PIT tag codes with a time stamp. Two systems were functional during the time of this study, one at AFTC (upstream of the hatchery release and effect site; downstream of all other wild fish tagging) and one approximately 1 km downstream of AFTC (downstream of all fish tagging and the hatchery release site) (Fig. 1). When used in combination, the two systems had an overall detection efficiency of 97% (91%–100%). The downstream antenna system had an antenna efficiency of 84%–97% (Zydlewski et al. 2003).

Results

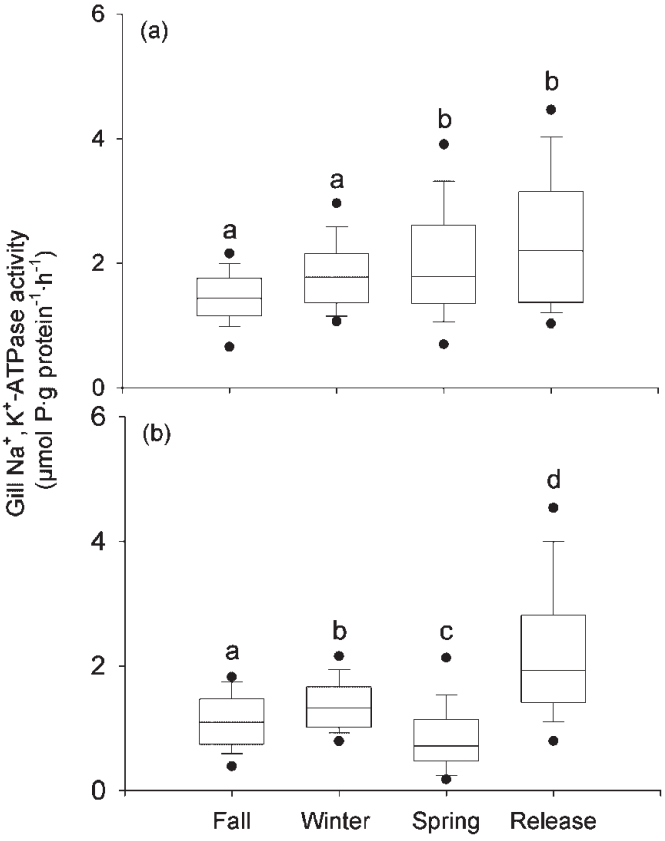
Fish

Wild steelhead averaged 129 ± 24 mm and 18 ± 13 g at the time of tagging (September and October) in 2003 and 122 ± 18 mm and 20 ± 14 g in 2004. Hatchery fish averaged 150 ± 20 mm and 36 ± 13 g at the time of tagging (January) in 2003 and 164 ± 48 mm and 27 ± 24 g in 2004.

Gill Na^+,K^+-ATPase levels in hatchery fish varied significantly throughout the year in 2003 and 2004, with the highest levels recorded in the hatchery on the day of release (Fig. 2). Differences among raceways were not significant in 2003 or 2004.

Steelhead trout density was similar in the control and effect sites before the release of hatchery fish. Wild steelhead trout density in the control site was estimated to be 6×10^{-4} fish·m^{-2} in 2003 and 5×10^{-4} fish·m^{-2} in 2004. Wild steelhead trout density in the effect site was 6×10^{-4} fish·m^{-2} in 2003 and 3×10^{-4} fish·m^{-2} in 2004. Lower densities in the effect site in 2004 were likely due to lower catch rates because of high water during sampling.

Fig. 2. Gill Na^+,K^+-ATPase activity of hatchery steelhead trout (*Oncorhynchus mykiss*) before release in April and May of (*a*) 2003 and (*b*) 2004. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) among seasons.



Body size and physiology

Hatchery steelhead trout were significantly larger (FL and weight) than wild steelhead trout migrating during the same period in 2003 and 2004 (Table 2). In 2003, there was no difference in size among the three release blocks. In 2004, steelhead trout size did differ between the three release blocks; wild and hatchery fish captured during the first release group were significantly larger than those caught later in the season for both hatchery and wild fish (Table 2).

Gill Na^+,K^+-ATPase activity was significantly lower in hatchery fish than in wild fish in all release blocks in both 2003 and 2004 (Fig. 3; Table 2). No differences were detected among the release blocks in 2003. In 2004, hatchery steelhead trout in the first release group had significantly lower gill Na^+,K^+-ATPase than hatchery fish from the third release (Fig. 3; Table 2).

Results from the seawater challenges conducted in 2004 revealed that hatchery migrants exposed to full-strength seawater consistently had significantly higher plasma [Na^+] ($P < 0.01$) and plasma osmolality ($P < 0.01$) than did wild migrants from the same trial (Fig. 4). This difference was

Table 2. Analysis of variance (rearing types are hatchery and wild; release blocks are three release dates) for fish FL, condition factor, and gill Na^+,K^+-ATPase activity for hatchery and wild steelhead trout (*Oncorhynchus mykiss*) captured at a screw trap on Abernathy Creek.

	2003			2004		
	F	df	*p*	*F*	df	*p*
Length						
Rearing type	78.3	1, 164	<0.01	58.5	1, 506	<0.01
Release block	1.59	2, 164	0.21	40.2	2, 506	<0.01
Rearing type by release block	0.31	2, 164	0.74	2.89	2, 506	0.06
Condition factor						
Rearing type	2.16	1, 164	0.14	54.3	1, 506	<0.01
Release block	1.56	2, 164	0.21	31.2	2, 506	<0.01
Rearing type by release block	2.43	2, 164	0.09	6.57	2, 506	<0.01
ATPase						
Rearing type	44.1	1, 164	<0.01	15.5	1, 506	<0.01
Release block	2.68	2, 164	0.07	10.3	2, 506	<0.01
Rearing type by release block	1.22	2, 164	0.30	0.36	2, 506	0.70

Fig. 3. Gill Na^+,K^+-ATPase activity of hatchery (open box) and wild (shaded box) steelhead trout (*Oncorhynchus mykiss*) caught in the screw trap in (*a*) 2003 and (*b*) 2004. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate the 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) among release blocks. Different numbers indicate statistical differences between rearing types.

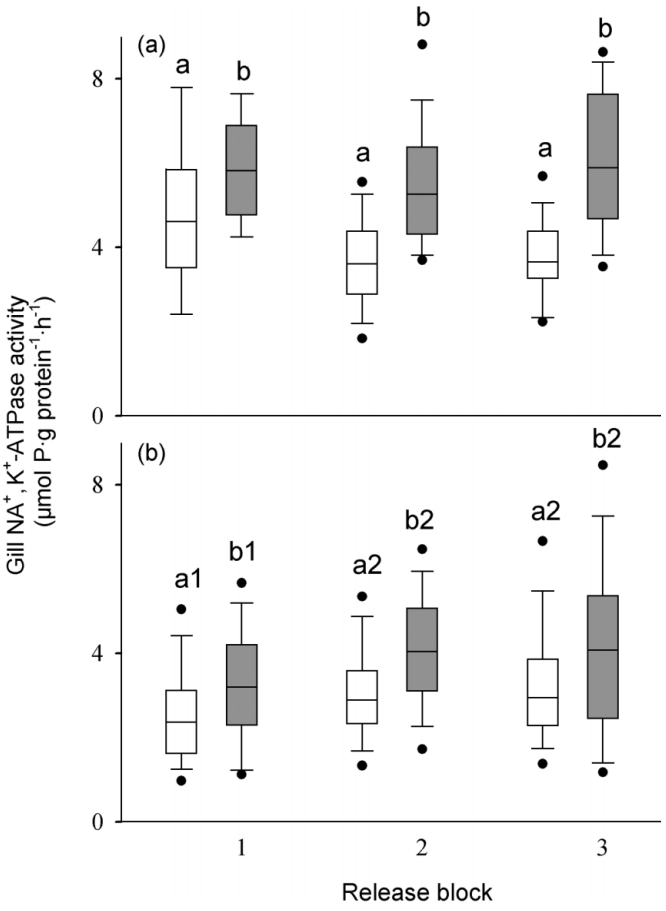


Fig. 4. Plasma (*a*) $[Na^+]$ and (*b*) osmolality of hatchery (open box) and wild (shaded box) steelhead trout (*Oncorhynchus mykiss*) exposed to a 24 h seawater challenge. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate the 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) within a release block.

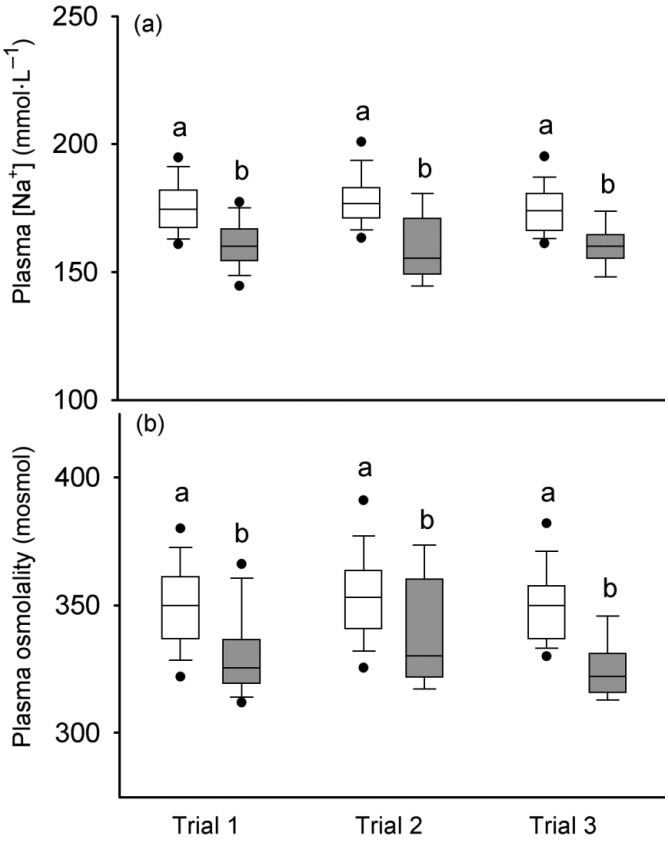
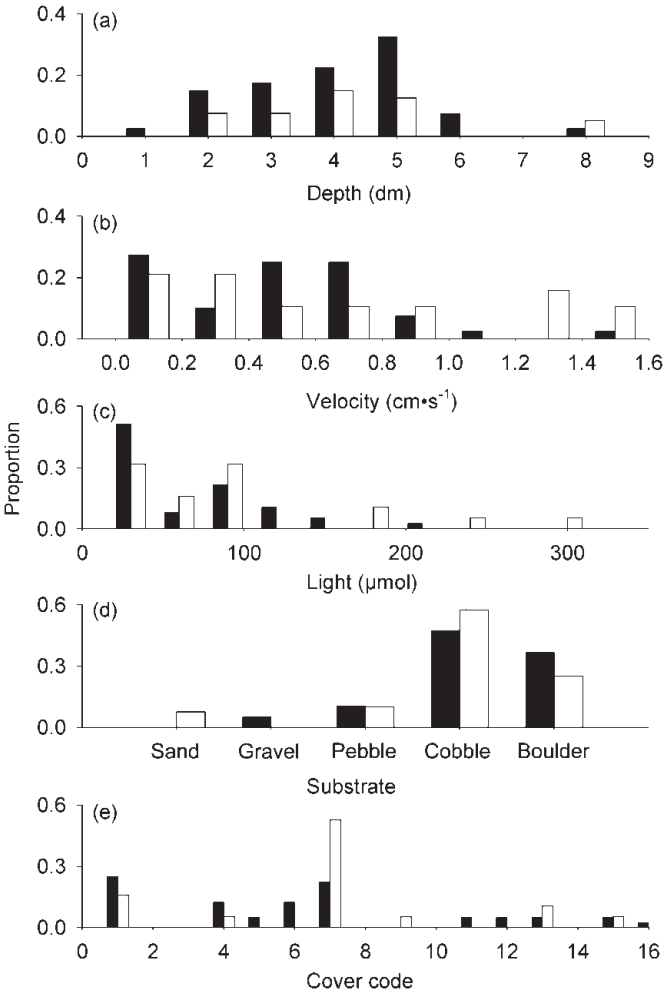


Table 3. Number of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) detected in the control and effect sites in 2003 and 2004.

	2003		2004	
	Hatchery	Wild	Hatchery	Wild
Control	0	11	1	47
Effect	18	48	13*	45

*Three of these fish were hatchery fish released in 2003 (resident hatchery fish).

Fig. 5. Distribution of habitat use for hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) detected in 2003. Detections in each habitat class ((*a*) depth, (*b*) velocity, (*c*) light, (*d*) substrate, and (*e*) cover) are displayed as proportions of the total detections.

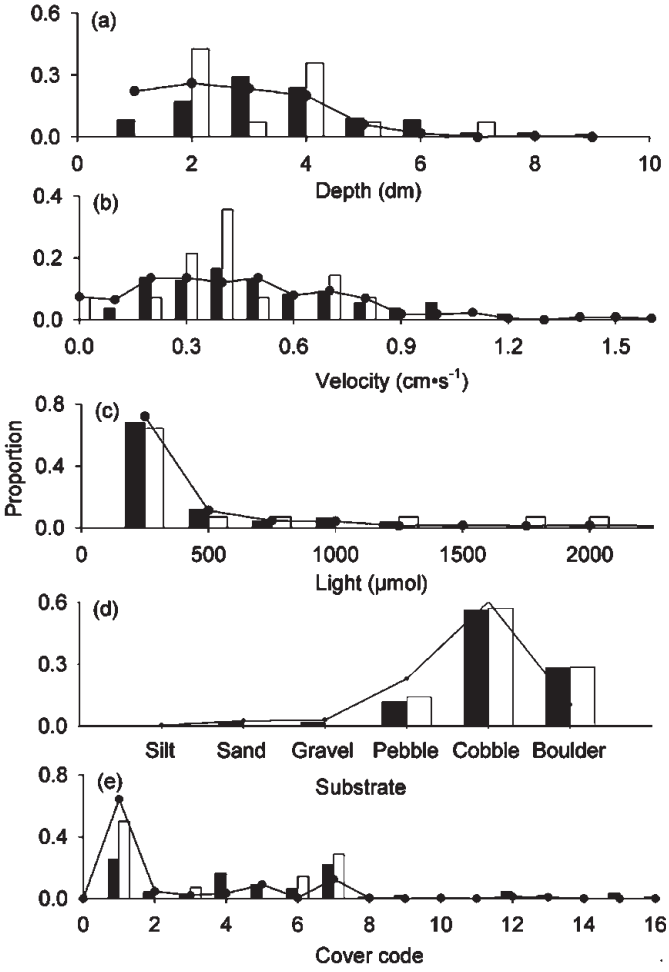


significant for all release blocks and did not change through the season. There was no significant tank effect for plasma $[Na^+]$ or plasma osmolality in any of the release blocks.

Habitat availability

The habitat available in May 2003 and May 2004 in the control and effect sites was similar. No significant differences were found in water depth, velocity, substrate, or cover. There was more shading available in the control site, when compared with the effect site, in 2003 and 2004 (F = 8.64, p = 0.005). The habitat available between years was also similar, differing only in light availability. There was significantly less shading available in 2004 compared with 2003 (F = 8.97, p = 0.004). All habitat units (riffle, run, glide, pool) were available during both years in both sites.

Fig. 6. Distribution of habitat use by hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) detected in 2004. Detections in each habitat class ((*a*) depth, (*b*) velocity, (*c*) light, (*d*) substrate, and (*e*) cover) are displayed as proportions of the total detections. Habitat types randomly available to steelhead trout in 2004 are indicted by a line and solid circle.



Habitat use

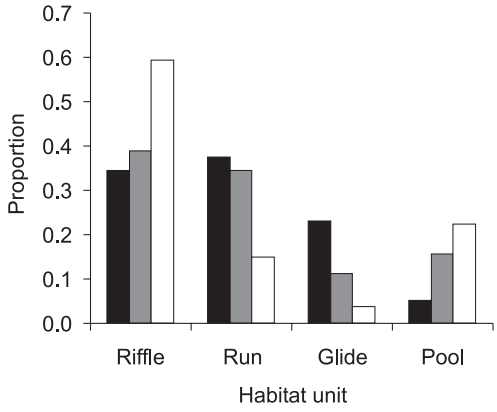
Fish were detected in all habitat types. A total of 183 individual fish were detected with PITpacks in the control and effect sites (Table 3). Fish use of the water column, substrate, and cover differed significantly from randomly available habitat. However, fish use of light and velocity did not differ from randomly available habitat. Wild fish used deeper water, larger substrate, and more cover than the randomly available habitat (Figs. 5, 6); whereas hatchery fish habitat use did not differ from the randomly available habitat (Table 4). Steelhead used riffles and pools more than were ran-

Table 4. Analysis of variance (ANOVA) for the use of habitat by hatchery and wild fish and the average habitat available.

	ANOVA		Percent difference between groups			
			Hatchery v. available		Wild v. available	
	F	*p*	Detected	Detectable	Detected	Detectable
Depth	15.0	<0.01	18	80	**20**	**8.7**
Flow	0.13	0.88	4.6	24	1.5	23
Surface light	0.30	0.74	5.2	8.1	2.4	4.2
Underwater light	0.52	0.59	8.7	306	4.5	110
Substrate	8.10	<0.01	12	29	**9.4**	**9.3**
Cover	24.5	<0.01	34	152	**94**	**55**

Note: Significant *F* values indicate that at least one group is significantly different from the others (df = 2, 351). The power analysis reveals where these differences occur and the percent difference that would be necessary to reject the null hypothesis. The percent difference between the groups detected by ANOVA is indicated in the "detected" column. The "detectable" column is the percent difference that would be required for a significant result based on the power ($\alpha = 0.05$, $\beta = 0.10$) of the performed tests, differing values for hatchery and wild fish are a result of sample sizes ($n = 15$ and $n = 100$, respectively). Significant results are in bold.

Fig. 7. Proportion of riffles, runs, glides, and pools used by hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) compared with the habitat available (shaded bar) in 2004.

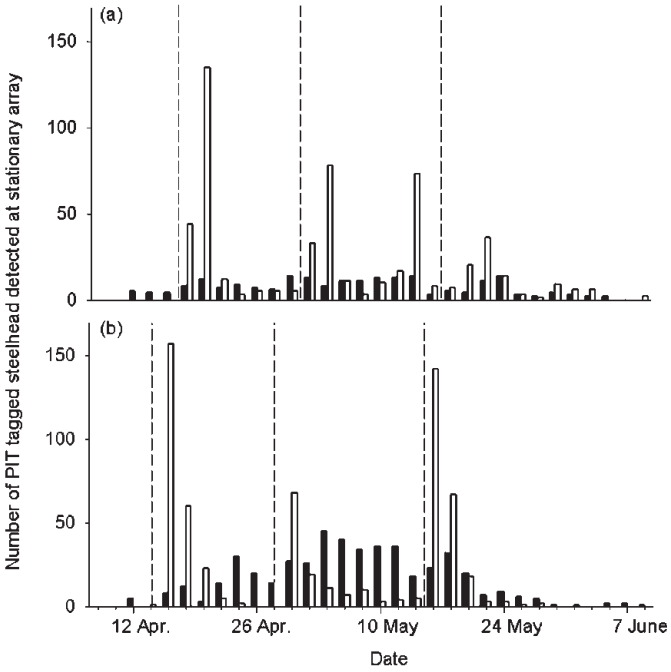


domly available, pools at levels lesser than found randomly in Abernathy Creek, and glides at similar levels as randomly available (hatchery, $\chi^2 = 182$, df = 3, $p < 0.01$; wild, $\chi^2 = 4.8$, df = 3, $p < 0.01$; Fig. 7). Hatchery and wild fish used habitat units similarly ($\chi^2 = 6.40$, df = 3, $p = 0.90$; Fig. 7).

The mean difference in velocity, depth, light, substrate, and cover use between hatchery and wild fish did not exceed 10%. However, some nonsignificant differences in the distribution of habitat use are notable (Figs. 5, 6). In 2003, 36.8% of hatchery fish were found in high-velocity (>0.7 cm·s^{-1}) habitats; 12.5% of wild fish were found at these velocities. In 2004, hatchery and wild fish used high-velocity habitats similarly. Hatchery fish were detected in six different cover combinations in 2003 and four in 2004; wild fish were detected in 10 cover combinations in 2003 and 12 in 2004. In 2003, hatchery fish were found under surface turbulence 52.6% of the time; wild fish used this cover less frequently (22.5%). Habitat differences were not evident when all habitat characteristics were considered simultaneously in the multivariate analysis, MDS ordination.

The BACI analysis did not reveal a significant change in wild fish habitat use after the release of hatchery fish relative to before release for water depth, velocity, surface light, underwater light, substrate, or cover in 2004 ($p \geq 0.16$). In addition, the main effects were not significant for any of the habitat characteristics. There was no difference in habitat use by wild fish during the before and after groups ($p \geq 0.12$) or between the control and effect sites ($p > 0.08$). High water prevented us from collecting an adequate before sample in 2003.

Fig. 8. Portable integrated transponder (PIT) tag detections of hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) at the stationary PIT array downstream of the effect site on Abernathy Creek in (*a*) 2003 and (*b*) 2004. Vertical broken lines indicate release dates.



Fish emigration

Hatchery and wild steelhead trout were detected at the downstream stationary antenna array on Abernathy Creek (Fig. 8). In 2003, 540 hatchery and 245 wild steelhead trout

were detected. In 2004, 1085 hatchery and 472 wild steelhead trout were detected. In both years, hatchery fish movement peaked the night of or day after release, whereas wild smolt movements were observed more consistently throughout the season.

Discussion

Hatchery and wild steelhead trout differed both physiologically and morphologically. Hatchery fish caught at the screw trap were larger but had lower levels of gill Na^+,K^+-ATPase activity when compared with wild fish caught at the same time. In 2004, a subsample of hatchery and wild fish caught at the screw trap were subjected to 24 h saltwater challenges. These challenges confirmed the gill Na^+,K^+-ATPase sampling results: wild fish performed better in saltwater when compared with hatchery fish, as indicated by higher gill Na^+,K^+-ATPase activity, and had better regulation of plasma [Na^+] levels and osmolality. Morphometric data on the released fish reveal that hatchery fish are shaped differently than wild fish (B. Kennedy, G.B. Zydlewski, K. Ostrand, and W.L. Gale, US Fish and Wildlife Service, AFTC, 1440 Abernathy Creek Road, Longview, WA 98632, USA, unpublished data). These results are consistent with those of other studies that found that hatchery fish were larger and shaped differently than wild fish (Swain et al. 1991) and had reduced levels of gill Na^+,K^+-ATPase activity (McCormick and Björnsson 1994).

Lower levels of gill Na^+,K^+-ATPase activity and reduced seawater tolerance of hatchery fish as compared with wild fish may impact the ability of hatchery fish to survive in the ocean environment. Gill Na^+,K^+-ATPase is a membrane-bound enzyme that acts as an ion pump transferring intracellular Na^+ in exchange for extracellular K^+ ions (for reviews, see de Renzis and Bornancin 1984; McCormick 1995 and Marshall and Bryson 1998). In the developing freshwater smolt, this enzyme increases in activity in preparation for transfer to the marine environment (Zaugg and McLain 1972; Rodgers et al. 1986; McCormick et al. 2003). This increase in ATPase activity is necessary for successful osmoregulation in seawater and generally occurs in the period before and during downstream migration (Zaugg et al. 1985; Rodgers et al. 1986; McCormick et al. 2003). Several studies have linked reduced smolt survival with decreased osmoregulatory status and other indicators of smolt development such as hormone levels and migratory tendency (Zaugg 1989; Muir et al. 1994; Beckman et al. 1999). Whether the physiological differences observed in this study will translate into differences in smolt survival remains to be tested.

Size (Spina 2003) and shape (Bisson et al. 1988) can affect fish habitat use. However, the different size and shape of Abernathy Creek hatchery and wild fish did not result in consistently different habitat use. Hatchery and wild steelhead trout in this study did not differ significantly in their use of habitat characteristics (water depth, velocity, shading, substrate, and cover). Although the power of the statistical tests performed was low for determining differences in fish use of velocity, light, and cover, differences between the rearing types would have to exceed 30% for a significant result for these habitat characteristics. There was a less than 10% difference between hatchery and wild fish use of all measured characteristics. Similarly, the MDS did not reveal any clustering of hatchery and wild fish. The detected differences are small but may be biologically important and should be interpreted with caution because of the low power of the statistical tests.

Similar habitat use by hatchery and wild fish could be a function of habitat preferences or habitat availability. Hatchery and wild fish could display similar patterns of habitat use without showing a difference in habitat preference if both groups are using habitat at the same frequency as it is available. Therefore, hatchery and wild fish locations were compared with randomly available habitats of Abernathy Creek, which revealed that wild fish preferred deeper water, more cover, and larger substrate than is commonly available. Although our power to detect these preferences in wild fish was sufficiently high, our power was low for hatchery fish (because of reduced sample sizes beyond our control). The trends in hatchery (nonsignificant) and wild fish (significant) habitat preferences were similar. Therefore, hatchery and wild fish use of randomly available habitat does reveal similar habitat preferences.

When hatchery and wild fish use similar habitats, the potential for hatchery fish to displace wild fish exists (Riley et al. 2004). This is increasingly likely when hatchery fish are larger than wild fish (Rhodes and Quinn 1998), as in Abernathy Creek. No differences were found in wild fish habitat use after the release of hatchery fish. This may indicate that competition between hatchery and wild fish for habitat resources is not occurring during the days following the release of hatchery fish.

There are several possible explanations for the lack of displacement of wild fish. (*i*) Hatchery smolts are rapidly leaving freshwater and thus are not competing with wild fish. (*ii*) Hatchery and wild fish do not compete for habitat. This may occur if fish densities are low relative to randomly available habitat. (*iii*) Hatchery and wild fish do compete for habitat, but wild fish outcompete hatchery fish and thus are not displaced. (*iv*) Hatchery and wild fish are competing, but our methods did not reveal the competition.

The possibility that hatchery fish rapidly leave Abernathy Creek following release is supported by several data sources. First, detection of hatchery fish with the PITpacks was low compared with wild fish detections (23% and 13% of the fish detected were hatchery origin in 2003 and 2004, respectively). Second, stationary PIT tag antenna arrays located downstream of the hatchery release site detected large numbers of fish leaving the system within 12 h following each release (G.B. Zydlewski, M.S. Hill, W.L. Gale, and J.D. Zydlewski, unpublished data). Third, a relatively small proportion of the hatchery fish released were detected during summer PITpack surveys (after emigration should have been complete), 0.05% and 2.8% in 2003 and 2004, respectively (2.2% and 4.8% of the wild fish tagged each year were detected). Because the number of residualizing steelhead trout appears to be low, the potential impact on wild fish habitat use is also likely low. The ecological effects on the wild population from hatchery residuals cannot be dismissed and warrant further investigation.

PIT-tagged fish (hatchery and wild) were seldom found close (<1 m) together during PITpack surveys, indicating low levels of interaction between fish. Abernathy Creek's

smolt production may be below its carrying capacity so that habitat availability exceeds habitat use. The carrying capacity of Abernathy Creek has not been determined, but can be approximated using the formula of Grant and Kramer (1990) (percent habitat saturation (PHS) = $100(\Sigma_{i=1}^{n} D_i + T_i)$, where D_i is density (fish·m^{-2}) and T_i is territory size). The steelhead trout density in Abernathy Creek, based on an annual smolt escapement of 4000 – 11 000 smolts (Patrick Hanratty, WDFW, 600 Capitol Way North, Olympia, WA 98501-1091, USA, unpublished data), is estimated at 0.02–0.06 steelhead trout·m^{-2}. The release of 20 000 steelhead trout smolts would raise the densities to 0.39–0.43 steelhead trout·m^{-2} downstream of the hatchery release site. Using these density values and territory sizes reported by Grant and Kramer (1990), it appears that Abernathy Creek likely remained below habitat saturation (39%–86% PHS) after hatchery releases, despite an increase in steelhead density. Therefore, it is likely that Abernathy Creek steelhead trout are not habitat-limited as a result of high fish densities. Determining a more accurate carrying capacity specific to Abernathy Creek is an important next step to the success of the native broodstock supplementation program.

The conclusion that steelhead trout are not habitat-limited is also supported by the preliminary work conducted in the control and effect sites, which shows a range of available habitat types from optimal (as indicated by wild fish presence) to suboptimal (as indicated by lack of presence). If habitat were limited, increasing use of suboptimal habitats with the increased smolt densities would be expected. A shift in habitat use was not revealed in the BACI analysis despite the range of habitats available.

If habitat were limited, a prior-residence advantage may have allowed wild fish to quickly defeat hatchery fish during competitions for optimal habitat. Support for this hypothesis from the literature is equivocal. The prior-resident effect has been demonstrated in similarly sized wild Atlantic salmon (*Salmo salar*; Huntingford and Garcia de Leaniz 1997) and hatchery and wild brown trout (*S. trutta*; Deverill et al. 1999). However, Rhodes and Quinn (1998) found that when the intruding fish was significantly larger (>6% difference) or of hatchery origin (and larger), it dominated the prior resident. We have no evidence to support competition for habitat between hatchery and wild fish at this time, although this possibility cannot be ruled out. In 2004, three "resident" hatchery fish, steelhead trout that had been released in 2003, were detected in spatially separated habitats with similar characteristics to other wild fish detection locations. With increased sampling effort and continuance of the program, it will be possible to discern whether prior residence is playing a role in the ability of wild fish to maintain their habitat. Levels of competition may increase in subsequent years as additional fish are released and remain in Abernathy Creek.

Fourth, the statistical and field methods employed may not have revealed hatchery and wild fish interactions. A power analysis of the BACI procedure revealed that power was below desirable levels for most habitat characteristics (except surface and underwater light). Low power is an issue common to unreplicated BACI designs; power can be improved with additional control or effect sites and an increase in sampling periods (Underwood 1992). A more rigorous BACI design would include multiple control sites (Underwood 1992). In this study, the control site was not replicated because of logistics. Instead, an effort was made to insure that the control and effect sites were similar for all measured parameters. Also, in 2004, the number of PIT-tagged fish, sampling effort, and performance of the PITpacks were improved to boost the sample size. Despite these improvements, the number of fish detections remained relatively constant. Detections likely remained low because the majority of smolts rapidly emigrated from the study site. Because these rapidly emigrating fish are not available for detection, increases in sampling effort may not result in significantly larger sample sizes. In addition, high levels of individual fish variation and daily variation in the stream environment make shifts in wild fish habitat use difficult to detect.

It is possible that differences between hatchery and wild fish occur on spatial and temporal scales that were not measured. Five habitat characteristics were quantified, all during the day. These characteristics were chosen because the majority of the literature recognizes water depth, velocity, substrate, and cover as critical to the distribution and abundance of salmonids (Armstrong et al. 2003). Salmonids typically seek protective habitat during the day when they are least active (Armstrong et al. 2003). As mentioned above, the availability of protective habitat may be in excess of that needed under the current densities. However, competition may still be occurring for other resources (Armstrong et al. 2003) or during the evening hours when steelhead trout are more active (Bradford and Higgins 2001). Sampling was conducted exclusively during the day because of the difficulties of employing the new PITpacks in a large stream. Day sampling methods are consistent with those of the majority of other salmonid field researchers (McMichael et al. 1999; McMichael and Pearsons (2001) included one night survey; Riley et al. 2004). PIT pack surveys during dawn and dusk may yield different results.

PIT tag technology has not previously been used to assess habitat use. Using PITpacks, habitat measurements are recorded without handling or often even viewing the fish. Because the fish is not seen at the time of detection, fish rearing type is unknown at detection and thus fish observations are unbiased. Although the technique minimizes disturbance to the fish, it creates the possibility for inaccurate habitat measurements. A rigorous comparison of habitat measurements recorded for fish detected by PITpack and more traditional methods, i.e., snorkeling, is a necessary next step. However, the PITpack method was not employed blindly. Fish were observed in an artificial stream and in Abernathy Creek to ensure that the PITpack had minimal effect on fish behavior and habitat choices (Hill et al. 2006). Results of these tests increase our confidence that the similarities between hatchery and wild fish were not due to methodology bias. In addition, if PITpacks were not detecting fish accurately in their microhabitats, no difference would be expected between the randomly chosen locations and the fish detection locations. Yet, differences greater than 10% between wild fish detected with PITpacks and the average habitat available were recorded for depth, cover, and substrate. In addition, fish were detected in areas similar to those reported for other salmonids (Armstrong et

al. 2003); this would not be expected if PITpack surveys were not a viable method for quantifying habitat use.

Our result that hatchery smolts in Abernathy Creek use habitats similar to those of their wild counterparts for the short time that they reside in the creek and do not displace wild fish is important. Other studies in the months following hatchery releases have found higher levels of residualism and competition in smolts (McMichael et al. 1999; McMichael and Pearsons 2001) and differing habitat use by wild steelhead trout of earlier life stages after the release of hatchery Chinook and coho salmon smolts (Riley et al. 2004). Different hatchery rearing practices may partially explain these disparate results.

Although few details are provided about the origin of the hatchery steelhead trout used by McMichael et al. (1999), McMichael and Pearsons (2001), and the hatchery Chinook and coho salmon smolts used by Riley et al. (2004), all were supplied by WDFW hatcheries and have most likely been in captivity for more than one generation. In contrast, the Abernathy Creek hatchery fish are a first-generation native broodstock and, as a result, are genetically indistinguishable from their wild counterparts (W. Ardren, US Fish and Wildlife Service, AFTC, 1440 Abernathy Creek Road, Longview, WA 98632, USA, personal communication 2004). However, the hatchery fish were reared under traditional hatchery conditions. These differences from wild rearing conditions in some cases are sufficient to cause differences in physical attributes and behavior. Hatchery rearing of Pacific salmon in the Northwest US has become more contentious as wild stocks continue to decline. The data generated by the current study provide a useful starting point for future studies examining the role of hatchery rearing practices on the behavior, habitat use, morphology, and physiology of hatchery fish with the idea of rearing more successful smolts. Further, it will be of great interest to see if these changes to hatchery rearing practices will result in a change in the level of hatchery–wild fish interactions.

Acknowledgements

The findings and conclusions in this report are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Data collection and reporting for 2003 were funded through the Bonneville Power Administration and the US Fish and Wildlife Service Student Career Experience Program. Data collection and reporting for 2004 were funded by the US Fish and Wildlife Service Oregon State Office. We thank Don Campton, Jeff Poole, Michele Grooms, Paul Larson, and John Holmes for spawning, handling, and maintaining hatchery broodstock and their progeny. We thank many people for helping in the PITpack surveys, habitat assessment, and electrofishing: John Holmes, Casey Jackson, Jeff Hogle, John Brunzell, Jeff Johnson, Joe Zydlewski, Christiane Winter, Troy Brigham, and others. We thank Danielle Warner and Bill Ardren for attempting to run parentage analysis on juveniles collected from Abernathy Creek in fall 2003. We thank the WDFW screw-trap crew: Pat Hanratty, Steve Wolthausen, Bryan Blazer, Brandon Bryant, and Brad Allen. We thank Brian Tissot, Cheryl Schultz, and Patty Crandell for reviewing the manuscript.

References

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. **62**: 143–170.

Bain, M.B., and Stevenson, N.J. 1999. Aquatic habitat assessment: common methods. American Fisheries Society, Bethesda, Md.

Baltz, D.M., Vondracek, B., Brown, L.R., and Moyle, P.B. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Trans. Am. Fish. Soc. **120**: 166–176.

Beckman, B.R., Dickhoff, W.W., Zaugg, W.S., Sharpe, C., Hirtzel, S., Schrock, R., Larsen, D.A., Ewing, R.D., Palmisano, A., Schreck, C.B., and Mahnken, C.V.W. 1999. Growth, smoltification, and smolt to adult return of spring Chinook salmon from hatcheries in the Deschutes River, Oregon. Trans. Am. Fish. Soc. **128**: 1125–1150.

Beckman, B.R., Larsen, D.A., and Dickhoff, W.W. 2003. Life history plasticity in Chinook salmon: relation of size and growth rate to autumnal smolting. Aquaculture, **222**: 149–165.

Berejikian, B.A. 1994. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. Can. J. Fish. Aquat. Sci. **52**: 2476–2482.

Bisson, P.A., Sullivan, K., and Nielsen, J.L. 1988. Channel hydraulics, habitat use and body form of juvenile coho salmon, steelhead and cutthroat trout in streams. Trans. Am. Fish. Soc. **117**: 262–273.

Bradford, M.J., and Higgins, P.S. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **58**: 365–374.

de Renzis, G., and Bornancin M. 1984. Ion transport and gill ATPases. *In* Fish physiology. Vol. 10B. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, Orlando, Fla. pp. 98–104.

Deverill, J.I., Adams, C.E., and Bean, C.W. 1999. Prior resistance, aggression, and territory acquisition in hatchery-reared and wild brown trout. J. Fish Biol. **55**: 868–875.

Fleming, I.A., Jonsson, B., and Gross., M.R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Fish. Aquat. Sci. **51**: 2808–2824.

Gatz, A.J., Sale, M.J., and Loar, J.M. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia, **74**: 7–19.

Grant, J.W., and Kramer, D.L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. **47**: 1724–1737.

Grau, E.G., Specker, J., Nishioka, R.S., and Bern, H.A. 1982. Factors determining the occurrence of the surge in thyroid activity in salmon during smoltification. Aquaculture, **28**: 49–57.

Harache, Y., Bouef, G., and Lasserre, P. 1980. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. III. Survival and growth of juvenile coho salmon transferred to sea water at various times of the year. Aquaculture, **19**: 253–273.

Hill, M.S., Zydlewski, G.B., Zydlewski, J.D., and Gasvoda, J.M. 2006. Development and evaluation of PIT tag detection units: PITpacks. Fish. Res. **77**: 102–109.

Huntingford, F.A., and Garcia de Leaniz, C. 1997. Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. J. Fish Biol. **51**: 1009–1014.

Kostow, K.E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. Can. J. Fish. Aquat. Sci. **61**: 577–589.

Leonard, J.B.K., and McCormick, S.D. 2001. Metabolic enzyme activity during smolting in stream- and hatchery-reared Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **58**: 1585–1593.

Marshall, W.S., and Bryson, S.E. 1998. Transport mechanisms of seawater teleosts chloride cells: an inclusive model of a multifunctional cell. Comp. Biochem. Physiol. A, **119**: 97–106.

Mesa, M.G. 1991. Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. Trans. Am. Fish. Soc. **120**: 723–727.

McCormick, S.D. 1993. Methods for nonlethal gill biopsy and measurement of Na^+,K^+-ATPase activity. Can. J. Fish. Aquat. Sci. **50**: 656–658.

McCormick, S.D. 1995. Hormonal control of gill Na^+,K^+-ATPase and chloride cell function. *In* Fish physiology. Vol. 14. *Edited by* C.M. Wood and T.J. Shuttleworth. Academic Press, San Diego, Calif. pp. 285–315.

McCormick, S.D., and Björnsson, B.Th. 1994. Physiological and hormonal differences among Atlantic parr and smolts reared in the wild, and hatchery smolts. Aquaculture, **121**: 235–244.

McCormick, S.D., Moriyama, S., and Björnsson, B.Th. 2000. Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. Am. J. Physiol. Regulatory Integrative Comp. Physiol. **278**: R1352–R1361.

McCormick, S.D., O'Dea, M.F., Moeckel, A.M., and Björnsson, B.Th. 2003. Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. Aquaculture, **222**: 45–57.

McMichael, G.A., and Pearsons, T.N. 2001. Upstream movement of residual hatchery steelhead into areas containing bull trout and cutthroat trout. N. Am. J. Fish Manag. **21**: 943–946.

McMichael, G.A., Pearsons, T.N., and Leider, S.A. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. N. Am. J. Fish. Manag. **19**: 948–956.

Muir, W.D., Giorgi, A.E., and Coley, T.C. 1994. Behavioral and physiological changes in yearling Chinook salmon during hatchery residence and downstream migration. Aquaculture, **127**: 69–82.

National Marine Fisheries Service. 2003. Hatchery broodstock summaries and assessments for chum, coho, chinook salmon and steelhead stocks within Evolutionary Significant Units listed under the Endangered Species Act, May 12, 2003. Salmon and Steelhead Hatchery Assessment Group (SSHAG). Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, and Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA.

Peery, C.A., and Bjornn, T.C. 2000. Dispersal of hatchery-reared Chinook salmon parr following release into four Idaho streams. N. Am. J. Fish. Manag. **20**: 19–27.

Rhodes, J.S., and Quinn, T.P. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. J. Fish Biol. **53**: 1220–1230.

Riley, S.C., Fuss, H.J., and LeClair, L.L. 2004. Ecological effects of hatchery-reared juvenile chinook and coho salmon on wild juvenile salmonids in two Washington streams. N. Am. J. Fish. Manag. **24**: 506–517.

Rodgers, J.D., Ewing, R.D., and Hall, J.D. 1986. Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **44**: 452–457.

Scheffe, H. 1959. The analysis of variance. Wiley and Sons, New York. pp. 331–369.

Simonson, T.D., Lyons, J., and Kanehl, P.D. 1994. Quantifying fish habitat in streams: transect spacing, sample size and a proposed framework. N. Am. J. Fish. Manag. **14**: 607–615.

Spina, A.P. 2003. Habitat associations of steelhead trout near the southern extent of their range. Calif. Fish Game, **2**: 81–95.

Swain, D.P., Riddell, B.E., and Murray, C.B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*) environmental versus genetic. Can. J. Fish. Aquat. Sci. **47**: 566–571.

Symons, P.E.K. 1969. Greater dispersal of wild compared with hatchery-reared juvenile Atlantic salmon released in streams. J. Fish. Res. Board Can. **26**: 1867–1876.

Underwood, A.J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable world. J. Exp. Mar. Biol. Ecol. **161**: 145–178.

Weber, E.D., and Fausch, K.D. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Can. J. Fish. Aquat. Sci. **60**: 1018–1036.

Zaugg, W.S. 1989. Migratory behavior of underyearling *Oncorhynchus tshawytscha* and survival to adulthood as related to prerelease gill (Na^+-K^+)-ATPase development. Aquaculture, **82**: 339–353.

Zaugg, W.S., and Mahnken, C.V.W. 1991. The importance of smolt development to successful marine ranching of Pacific salmon. *In* Marine Ranching: Proceedings of the 17th U.S.–Japan Meeting on Aquaculture. *Edited by* R.S. Svrjcek. NOAA Tech. Rep. No. NMFS 102. pp. 89–97.

Zaugg, W.S., and McLain, L.R. 1972. Changes in gill adenosinetriphosphatase activity associated with parr–smolt transformation in steelhead trout, coho and spring chinook salmon. J. Fish. Res. Board Can. **29**: 167–171.

Zaugg, W.S., Prentice, E.F., and Waknitz, F.W. 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. Aquaculture, **51**: 33–47.

Zippin, C. 1958. The removal method of population estimation. J. Wildl. Manag. **22**(1): 82–90.

Zydlewski, G.B., Winter, C., McClanahan D., Johnson J., Zydlewski J., and Casey S. 2003. Evaluation of fish movements, migration patterns, and population abundance with streamwidth PIT tag interrogation systems. Project No. 2001-01200, Bonneville Power Administration, Portland, Oregon. BPA Rep. No. DOE/BP-00005464-1.

Zydlewski, G.B., Haro, A., and McCormick, S.D. 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behaviour of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. **62**: 68–78.