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Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams?

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Hatchery and wild juvenile populations of steelhead *Oncorhynchus mykiss* and coho salmon *Oncorhynchus kisutch*, in a small coastal watershed in central California, were sampled throughout the year in a stream and at a hatchery. Both species grew faster in captivity than in the wild. Hatchery fish of both species had elevated gill Na^+, K^+ -ATPase activity, and thus were ready to enter sea water when planted during the wild fish migration. Downstream migrant trapping and stream surveys indicated that hatchery smolts went to sea soon after planting, consequently avoiding the effects of competition and predation that commonly occur when hatchery-bred juveniles are released. Adult steelhead were also sampled throughout the watershed. The return of hatchery steelhead was highly synchronized with that of wild steelhead, indicating that hatchery propagation had no adverse effects on the timing of the run. A disproportionate number of hatchery steelhead returned to the tributary where the hatchery was located, despite being planted throughout the watershed. Hatchery steelhead did not differ in mean age or size from wild steelhead. Observations of spawning indicated that hatchery and wild steelhead interbreed. Competition for mates or spawning substratum was rarely observed between hatchery and wild steelhead. Many of the problems commonly associated with artificial propagation can be avoided in small coastal watersheds when wild broodstock are used and fish are released as smolts.

Key words: coastal watershed; coho salmon; conservation; hatchery; steelhead; wild.

INTRODUCTION

Artificial propagation to supplement salmonid populations has increased in recent decades. These supplementation efforts are used to increase commercial harvest, raise 'farmed' fish, enhance sport fishing, compensate for habitat lost to dam construction and conserve endangered stocks.

Numerous studies have been conducted on the effects of hatchery production, ranging from analysis of large data sets across multiple populations to local ecological and genetic effects in a single river or laboratory experiment (Levin *et al.*, 2001; McGinnity *et al.*, 2003; Weber & Fausch, 2003). A common conclusion

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drawn from these studies is that artificial propagation of salmonids negatively affects the ecology, genetic structure and population dynamics of wild stocks.

Although many studies identify specific problems and suggest solutions, no studies have investigated the effects of artificial propagation in systems where such problems are being avoided or the proposed solutions have been implemented. As a result, the question of whether artificial propagation can be effective under ideal management conditions has not been tested. In addition, hatchery and wild salmonid interactions and the potential management solutions in very large rivers with long migration distances, often >100 km (Chilcote *et al.*, 1986; Levin & Williams, 2002), may differ greatly from those in small coastal watersheds with much shorter migration distances (Nickelson *et al.*, 1986; McLean *et al.*, 2003).

Stocking hatchery-produced juveniles in streams can lead to numerous consequences (Flagg *et al.*, 2000). Social behaviours of juvenile hatchery salmonids normally deemed maladaptive in natural settings could be favoured in an unnatural high-density situation like raceways or overstocked streams. Hatchery fishes grow faster than wild fishes and when put into streams they are significantly larger. In these situations hatchery-produced juveniles may out-compete wild fishes for resources or prey directly on wild juveniles. In response, wild fishes may grow more slowly and be forced into early migration, resulting in poorer survival (Nickelson *et al.*, 1986; McMichael *et al.*, 2000). Hatchery fishes may also stimulate predator abundance or change predator behaviour; thus wild fishes whose emigration coincides with hatchery releases may encounter more predators (Nickelson, 2003). Alternatively, wild fishes may encounter fewer predators because of dilution effects.

Despite a potential advantage associated with larger size in the early life stages, hatchery fishes may have lower reproductive success, because hatchery adults may be at a competitive disadvantage on the spawning grounds. Having undergone more intense natural selection, wild adult males may out-compete hatchery males when spawning (Berejikian *et al.*, 1997). Also, hatchery females nest-building behaviour may be inferior to that of wild females (Fleming *et al.*, 2000; McLean *et al.*, 2003). Finally, the timing of return for hatchery fishes is often not synchronized with the return of wild fishes, because hatcheries spawn the first fishes to return or use non-native stocks (Chilcote *et al.*, 1986; Leider *et al.*, 1986; Mackey *et al.*, 2001; McLean *et al.*, 2003).

For all of these reasons, recent recommendations often stress that management efforts should focus on the recovery of wild stock with minimal hatchery intervention (Hindar *et al.*, 1991; Waples, 1991; Myers *et al.*, 2004). Nonetheless, artificial propagation may be beneficial when stocks are severely depleted so it is still widely used to supplement wild populations. Because artificial propagation programmes are likely to continue in the foreseeable future, it is critical that the most effective hatchery practices be implemented and tested wherever interactions between hatchery and wild salmonids are likely to occur (Flagg & Nash, 1999).

This study compares hatchery and wild life histories and the ecological effects of hatchery-produced salmonids from a small conservation hatchery that is being used to rehabilitate wild stocks of steelhead *Oncorhynchus mykiss* (Walbaum) and coho salmon *Oncorhynchus kisutch* (Walbaum) in a small coastal watershed. Because both stocks are listed as threatened under the United States Endangered

Species Act (ESA) (Weitkamp *et al.*, 1995; Busby *et al.*, 1996, 2000), the hatchery is managed according to many commonly suggested protocols for reducing the negative effects of artificial propagation described above, and to promote free interbreeding of wild and hatchery spawners (Ewing *et al.*, 1995; Flagg & Nash, 1999; Flagg *et al.*, 2000). The objective of this study was to investigate how the wild populations are being affected by current artificial propagation techniques by investigating the potential for competition and predation between hatchery and wild juveniles and monitoring for differences between hatchery and wild spawning adults that would result in a shift away from natural population characteristics. This study was broken down into two main components: 1) behavioural, growth and physiological comparisons of hatchery and wild fish at the juvenile stage, and 2) measurements of adult reproductive behaviour and size.

MATERIALS AND METHODS

Scott Creek is a small coastal watershed in central California, 100 km south of San Francisco. Anadromous fish can access *c.* 23 km of stream between the estuary and natural upstream barriers of the main stem and the three main tributaries: Little Creek, Big Creek and Mill Creek (Fig. 1). A small estuary at the bottom of the watershed becomes a freshwater lagoon during summer, when low flows in combination with wave action result in the formation of a sandbar that isolates the stream from the ocean. Flows were measured on a cross-section of the main stem with a Marsh-McBirney, Inc. Flo-Mate Model 2000 Portable Flowmeter. A small California Department of Fish & Game (CDF&G) cooperative hatchery has been operated by a non-profit organization, the Monterey Bay Salmon and Trout Project (MBSTP), on the Big Creek tributary since 1982. Research was conducted throughout the portion of the watershed that was accessible to anadromous fishes.

HATCHERY PRODUCTION PROTOCOL

The standard production cycle for the hatchery began with collection of wild coho salmon from December 2001 to February 2002 and wild steelhead during February and March 2002. Wild adult fishes were captured by teams of divers and additional people blocking pool exits with dip-nets. The fishes were transported the short distance to the hatchery in an oxygenated holding tank and held in 4 m diameter $\times$ 1·5 m deep circular pools until they were ready to spawn. Upon capture, coho salmon females were injected with erythromycin (20 mg kg^{-1}) to prevent the spread of *Renibacterium salmoninarum*, associated with bacterial kidney disease. Likewise, steelhead females were injected with amoxicillin (40 mg kg^{-1}) to prevent the spread of *Flexibacter psychrophilum*, associated with bacterial coldwater disease.

A small piece of caudal fin was clipped from each fish for DNA analysis using 18 microsatellite loci. Due to the low genetic diversity in the coho salmon population, the degree of relatedness between fish was used to establish a pair-wise spawning matrix that optimizes genetic diversity in the hatchery offspring (Garza & Gilbert-Horvath, 2003). During spawning each female was cross-fertilized with two to four of the least related males. For steelhead, mating was random and each female was cross-fertilized with two to four males.

After fertilization, each female's eggs were placed in individual upwelling incubation jars until they reached the eyed stage. Eggs were then transferred to Heath Vertical Incubator Trays® until the 'swim-up' stage, maintaining one female's eggs per tray. Swim-up fry coho salmon were then transferred to deep troughs (0·61 $\times$ 9·75 m, 38 cm of water) while steelhead were transferred to standard CDF&G hatchery troughs (0·23 $\times$ 9·75 m, 10 cm of water), and family groups were combined. Trough densities

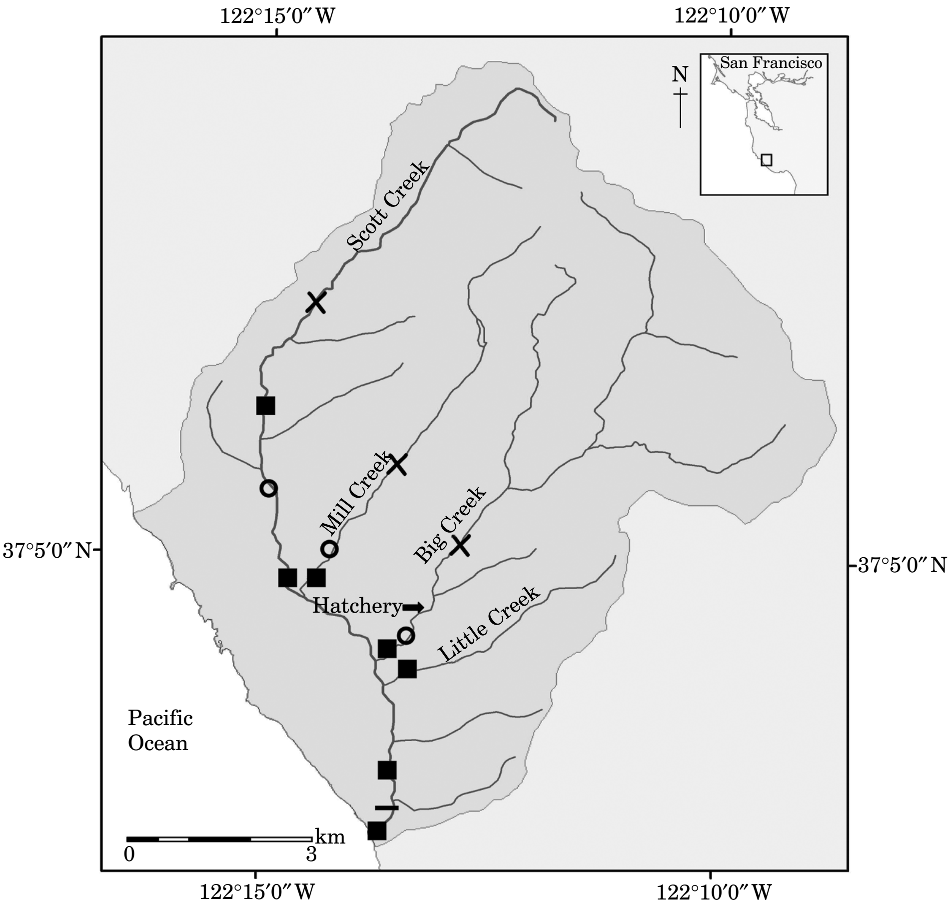

FIG. 1. Scott Creek watershed with relevant marked sites: planting locations (O), survey locations (■), natural barriers (X) and downstream migrant trap (▬).

were maintained at <16 000 fish per trough for coho salmon and <10 000 fish per trough for steelhead. Feeding began at the trough stage, when automatic feeders provided a commercially available dry salmon food (Sterling®, UT, U.S.A.) at a rate of *c*. 2% body mass per day.

Fishes were transferred to outdoor raceways or circular tanks under natural lighting when they reached a mean size of 1 g and remained there until being planted during the last week of March and first week of April the following year. Rearing densities prior to release were a maximum of 4 kg m^{-3}. Several months before release, all hatchery fishes were marked by removal of the adipose fin. Fish were planted at three locations throughout the upper watershed (Fig. 1).

JUVENILE PROTOCOL

Beginning in April 2002, downstream migrating fishes were trapped at the head of the estuary by means of a two-chambered 0·95 cm square mesh hoopnet with wings extending to each bank. The trap was operated 3 days per week throughout the year except during exceptionally high flows associated with winter storms. The number of fish passing through the trap was recorded by species and origin (hatchery or wild as determined by adipose fin presence or absence). Fish were sampled monthly at six locations throughout the upper watershed and at the hatchery with a $3 \times 1{\cdot}5$ m beach seine ($0{\cdot}32\,cm^2$ mesh). Fish in the estuary were captured with a 30×2 m beach seine ($0{\cdot}95\,cm^2$ mesh). Upon collection, fishes were temporarily placed in a holding container until processing.

During processing, up to 20 fish of each species and origin (wild or hatchery) at a given site were lightly anaesthetized with clove oil (dissolved in 80% ethanol at 1 : 9 ratio, final dosage $50\,mg\,l^{-1}$) and processed (Woody *et al.*, 2002). Fork length (L_F) measured to the nearest mm for each fish, and mass was recorded to the nearest 0·01 g. Scale samples were taken from steelhead at a common spot just posterior and ventral to the dorsal fin on the left side. Hatchery fishes (500 steelhead, 473 coho salmon) were injected with passive integrated transponder (PIT) tags at least 1 week before planting and rescanned at the downstream migrant trap to measure migration timing. In order to determine seawater readiness, gill filament samples were collected to measure Na^+, K^+ -ATPase activity from at least 10 hatchery fishes and 10 wild downstream migrants on a monthly basis during February to June 2003. Gill biopsies were collected on fish >100 mm and assayed in accordance with McCormick's non-lethal micro method (McCormick, 1993). Fishes were then placed in a recovery container for at least 10 min before release.

ADULT PROTOCOL

Because of the very small run size of coho salmon and concerns about the effects of handling, research on adult life history was limited to steelhead, which were readily available for study. Samples were taken throughout the watershed by teams of divers and additional people blocking pool exits with dip-nets. A few fish were collected in the downstream migrant trap or with seines. The installation of a fish trap in the autumn of 2003 made it possible to sample adults during the 2004 spawning run.

Upon capture, adults were placed in a soft, wet, mesh bag and processed immediately without anaesthesia. Fork length was recorded to the nearest 0·5 cm and mass was recorded to the nearest 0·02 kg. Scale samples for age analysis were taken from the left side just dorsal of the lateral line and posterior to the dorsal fin. Hatchery or wild origin was determined by the presence or absence of an adipose fin, and sex was determined from external characteristics and manual expression of the vent for sperm or eggs. An individually numbered Floy tag®, colour-coded to indicate origin and sex, was inserted at the posterior base of the dorsal fin. Fish were released to the stream after handling.

Spawning surveys were made between sunrise and sunset on an opportunistic basis along the Big Creek tributary between January and April in 2002, 2003 and 2004. When spawning was observed, data were collected on the specific location, time of day, the number of anadromous (typically >40 cm) and resident fish (typically <25 cm), fish origin, whether any fish were tagged, and relative size and rank when dominance interactions occurred.

SCALE ANALYSIS

Scales from adult steelhead were analysed to determine absolute age, and L_F at ocean entry. All scale samples were cleaned with ultrapure Milli-Q® water in a sonicating bath to remove mucus and debris. Clean scales were flattened between microscope slides and digitally microphotographed. Scale images were then analysed by means of OPTIMUS® software (Media Cybernetics- Carlsbad, CA) to measure scale radius (R_S), number and placement of annuli, the number of circuli, distance between circuli, and R_S at the time of ocean entry. Smolt size at initial ocean entry for each adult was determined using the Fraser–Lee method of back-calculation through a linear regression of L_F and R_S (Bartlett *et al.*, 1984; Ward *et al.*, 1989). Scale radius from 175 steelhead of known L_F (60–795 mm), were used to generate the regression.

STATISTICAL ANALYSIS

The GLM procedure in SAS® was used to test for significant differences in growth rates between hatchery and wild fish. The variance ratio test was used to test for differences in variance of size in returning adults (Zar, 1996). All remaining statistics were calculated using Systat® 10.2. Means are reported with ±S.E. Because the statistical tests varied with the nature of the data, details of specific tests are given in each section of the Results.

RESULTS

JUVENILE

Growth

Growth measurements were taken for the 2002 year class of wild coho salmon young-of-the-year [YOY; Table I and Fig. 2(a)]. Because almost all coho salmon go to sea after 1 year in the stream and since the 2001 and 2003 year classes were nearly extirpated, there was little overlap or confusion among year classes. Hatchery-raised coho salmon were on an accelerated growth regime during 2002, as part of a plan to induce some hatchery fish of both sexes to return from the ocean migration 1 year early and rebuild a nearly extirpated year class [Table I and Fig. 2(a)]. As a result, hatchery coho salmon grew faster in captivity (GLM, $P < 0{\cdot}001$) and were much larger than wild fish of the same year class at release. No growth data for hatchery coho salmon in the wild are available because none were found during this sampling period.

Comparison of growth rates between hatchery and wild steelhead from the 2002 year class was possible from April 2002 to March 2003 [Table I and Fig. 2(b)]. The highly variable life history of steelhead, however, made accurate distinction of the 2002 year class difficult in the field during the spring of 2003 as fast-growing members of the 2003 year class began to overlap in L_F with slow-growing members of the 2002 year class. Hatchery steelhead grew faster in captivity relative to YOY wild fish in the upper watershed and to age 1+ year wild smolts in the estuary (GLM, $P < 0{\cdot}001$). Thus hatchery steelhead were comparable in size at release to wild steelhead smolts of previous year classes

TABLE I. Regression results for growth rates of hatchery and wild coho salmon and steelhead in Scott Creek watershed

	Initial L_F (mm)	Growth rate (mm day^{-1})	r^2	n	Date range
Coho salmon					
Hatchery YOY	65·78 ± 0·79	0·309 ± 0·006	0·813	497	June 2002 to April 2003
Wild YOY	50·68 ± 0·44	0·139 ± 0·003	0·536	2190	June 2002 to April 2003
Steelhead					
Hatchery YOY	51·49 ± 0·77	0·438 ± 0·010	0·752	527	June 2002 to March 2003
Wild YOY	39·50 ± 0·71	0·114 ± 0·007	0·235	1563	June 2002 to March 2003
Wild smolt	107·08 ± 5·34	0·333 ± 0·013	0·300	730	April 2002 to November 2003

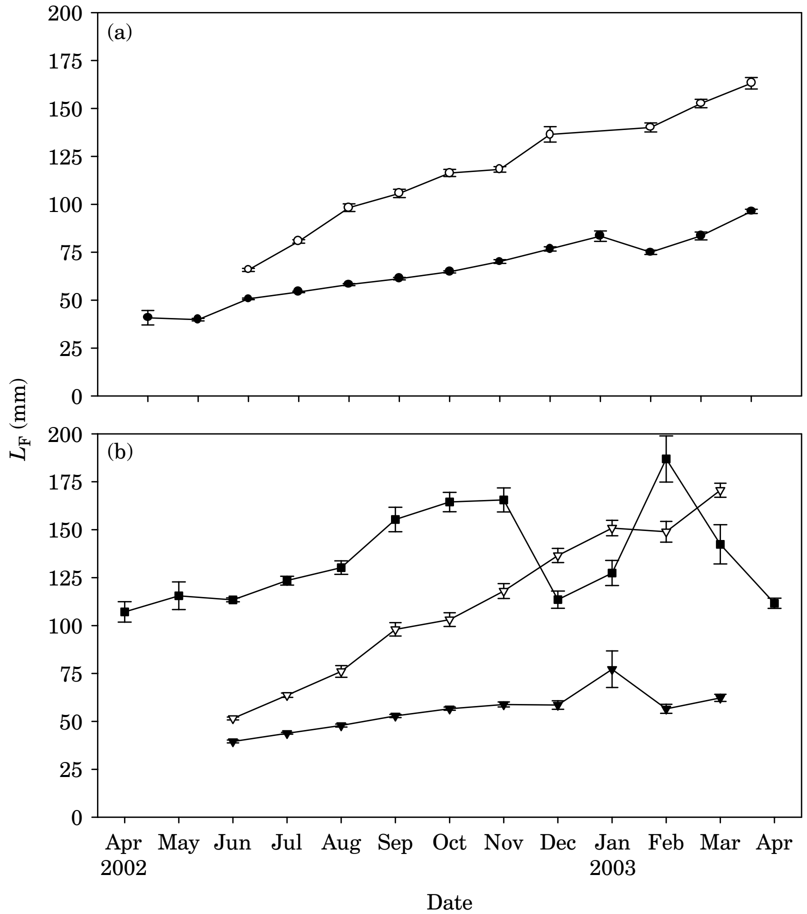

FIG. 2. Mean ± S.E. fork length for the 2002 Scott Creek year class from April 2002 to April 2003 for (a) hatchery (○) and wild (●) coho salmon YOY and (b) hatchery (▽) and wild (▼) steelhead YOY and wild steelhead smolts (■) from previous year classes sampled in the estuary and downstream migrant trap.

entering or living in the estuary [Fig. 2(b)]. No growth data were available for hatchery steelhead in the wild because none were found during this sampling period.

A large number of wild steelhead smolts remained in the estuary, which was closed to the ocean by a sandbar from 15 July 2002 to 8 November 2002 (Fig. 3). By the time the stream closed, all hatchery fish appeared to have entered the ocean, and there was little downstream migration of wild steelhead smolts into the estuary. Growth rates for steelhead smolts trapped in the estuary were faster than observed for wild YOY steelhead in the upper watershed [Table I and Fig. 2(b)]. Beginning in November, winter storms reopened the estuary, allowing summering smolts to depart and probably stimulating the downstream migration of smaller fish from the upper watershed into the estuary, causing a marked change in the size distribution of steelhead.

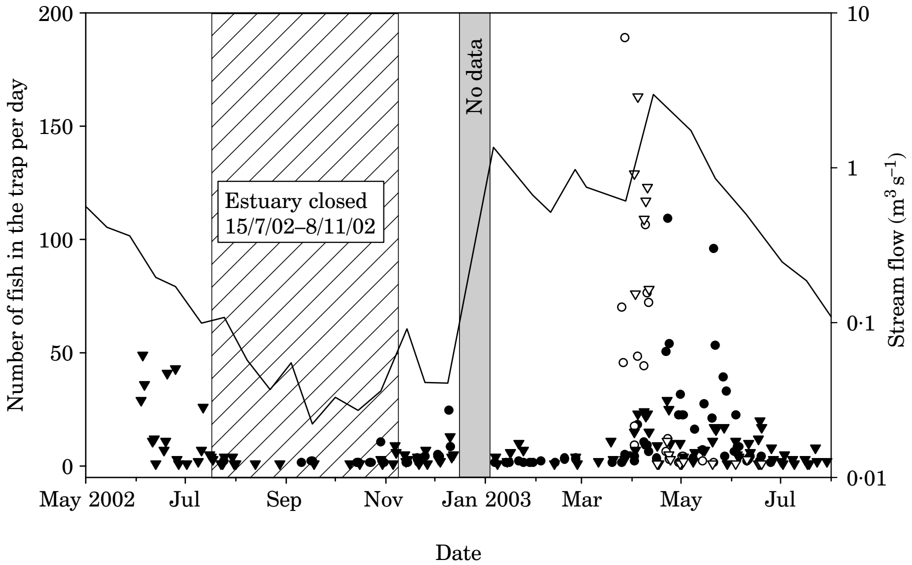

FIG. 3. Daily smolt counts from the downstream migrant trap in the lower Scott Creek just above the entrance to the estuary. Count data are included for hatchery coho salmon (○), wild coho salmon (●), hatchery steelhead (▽) and wild steelhead (▼). Stream flow (—) data for the lower Scott Creek mainstem are superimposed with reference to the right *y*-axis (log scaling). Flow data were collected twice per month and do not represent peak flows following storm events.

Instream distributions

Presence and distribution of juvenile hatchery and wild fishes was measured throughout the year. The hatchery planted 7200 steelhead and 3322 coho salmon in Scott Creek during the last week of March 2002. The last hatchery fish observed was a steelhead in the estuary on 2 May 2002. No hatchery fishes were observed in the downstream migrant trap or during 71 surveys conducted at seven locations (Fig. 1) throughout the watershed from June 2002 until the hatchery planted 7500 steelhead and 6600 coho salmon in March 2003. Approximately 2190 wild coho salmon and 2374 wild steelhead were observed during these same 71 surveys.

Downstream migration

Downstream migration of both species was monitored 3 days per week from June 2002 to August 2003 (Fig. 3). For a 2 week period during December 2002 to January 2003 the trap was not operated. Because of the weak year class there were no emigrating coho salmon in June 2002, but wild steelhead were migrating downstream. Steelhead migratory activity declined with flow and remained low during summer months. Low numbers of wild coho salmon and steelhead passed through the trap during autumn and winter. Emigration of wild steelhead juveniles began increasing in March 2003, peaked in April and May and declined into July. Coho salmon juveniles had a more restricted emigration, primarily late March and April. The hatchery fish of both species were planted in late March and moved downstream rapidly; most fishes passed through the trap within 1 month.

The number of outmigrating juveniles was estimated from data from the downstream migrant trap (Table II). Samples were taken only 3 days per week. A low estimate for the total number of wild smolts was determined by extrapolating to continuous sampling 7 days per week. From the known number of hatchery coho salmon and steelhead released, and from stream surveys indicating that virtually all hatchery fishes departed the system, catch efficiency of the trap was determined to be *c.* 11% of the total number of hatchery fish released for both species. This efficiency reflects a combination of trap evasion and mortality between release and emigration (there are no data on post-release survival for hatchery fishes in this system). On the basis of these catch efficiencies, a high estimate for total numbers of wild smolts migrating between September 2002 and September 2003 was determined.

In 2003, a sub-set of the hatchery coho salmon and steelhead were PIT tagged to measure the amount of time hatchery fish spent in the watershed before migrating to the ocean. Fish were given at least 1 week to recover from tagging before being released at typical planting sites for each species on 7 April 2003. The trap was checked each day for the first week after planting. Each hatchery fish was scanned for a PIT tag before being released below the net. Approximately 47% of the tagged coho salmon and 17% of the tagged steelhead had moved through the trap in the 4 days preceding a 4 day storm event that made trap operation impossible (Fig. 4). The remaining hatchery fishes either evaded the trap or were probably washed downstream by the storm, because only 0·08% of the tagged coho salmon and 1·2% of the tagged steelhead were observed after the storm. Accurate assessments were inhibited by the storm, but it appears that most of the coho salmon had moved downstream within 1 week of planting at a rate of $3 \cdot 28 \pm 0 \cdot 11$ km day^{-1} ($n = 224$), while the steelhead appeared to take longer (t-test, $P = 0 \cdot 001$), moving at a rate of $2 \cdot 68 \pm 0 \cdot 15$ km day^{-1} ($n = 91$). Migration speed was calculated for each resighted fish by dividing the distance travelled by the number of days required to travel from the planting sight to the trap and determining a mean for each species.

TABLE II. Estimated number of outmigrating juvenile steelhead and coho salmon in Scott Creek, September 2002 to September 2003. Reported are the total number of fish captured by a downstream migrant trap that was operated 3 days per week for 1 year, the total number of fish released by the hatchery that year, trap catch effectiveness and estimates of the number of wild smolts

	Coho Salmon		Steelhead	
	Wild	Hatchery	Wild	Hatchery
Total number caught	792	706	587	827
Hatchery fish released		6600		7500
Capture efficiency (%)		10·70		11·03
Wild smolt estimates				
Low[1]	1848		1370	
High[2]	7404		5323	

[1]Low estimates were based on extrapolating the 3 day week^{-1} catch effort to 7 day week^{-1}.
[2]High estimates applied capture efficiency to total number caught and extrapolating to a 100% capture efficiency.

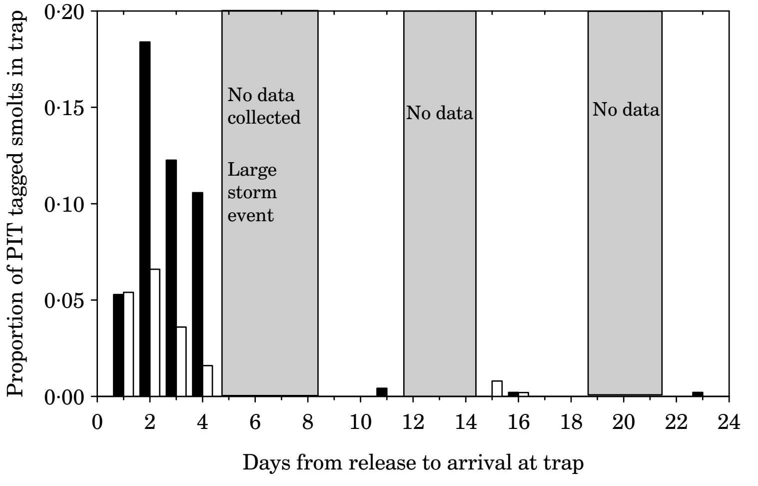

FIG. 4. Downstream travel time for hatchery coho salmon (■) and hatchery steelhead (□) following planting in Scott Creek watershed on 7 April 2003: 473 PIT-tagged coho salmon in the upper Scott Creek, 7·3 km from the estuary and 500 PIT tagged steelhead in the Big Creek, 4·7 km from the estuary.

Size at ocean entry

Measurements of steelhead captured at the downstream migrant trap did not directly indicate size at ocean entry, because many wild fish were observed to spend the summer in the estuary (downstream of the trap), and their exact departure dates and size were unknown. But repeated seine hauls throughout the watershed and the estuary indicated that hatchery steelhead entered the ocean soon after planting, and it is likely that little growth occurred after the last measurement taken before planting. Based on the Ward *et al.* (1989) method, scales collected from returning adult steelhead were analysed to determine the R_S at the ocean entry mark and backcalculate the size at ocean entry for hatchery and wild fish from the regression equation: $\ln L_F = 0{\cdot}8807\ln(R_S \text{ at ocean entry}) - 0{\cdot}7104$; $n = 175$, $r^2 = 0{\cdot}97$. There was no difference in relative size between hatchery and wild steelhead (192·6 *v.* 181·7 mm; $F_{1,52}$, $P = 0{\cdot}398$) or males and females (185·0 *v.* 187·3 mm respectively; $F_{1,52}$, $P = 0{\cdot}752$) for 2002 and 2003 returns. Of course, the actual size distribution of wild fish at ocean entry could not be determined because this technique used scales only from returning survivors. It was not possible to perform these analyses with coho salmon because returning adults were not sampled.

Smolt physiology (Na^+, K^+ -ATPase activity)

The Na^+, K^+ -ATPase activity levels in gill tissue were measured as an indicator of the degree to which fishes had undergone the physiological transformation associated with smoltification in preparation for entering sea water. Fish from each species and origin (hatchery *v.* wild) were compared for each of the 4 months surrounding the peak downstream migration as they passed through the downstream migrant trap and at the hatchery prior to release (Fig. 5). Analysis of variance with *post-hoc* Tukey adjustments for multiple comparisons was used to test between groups. Because the wild coho salmon

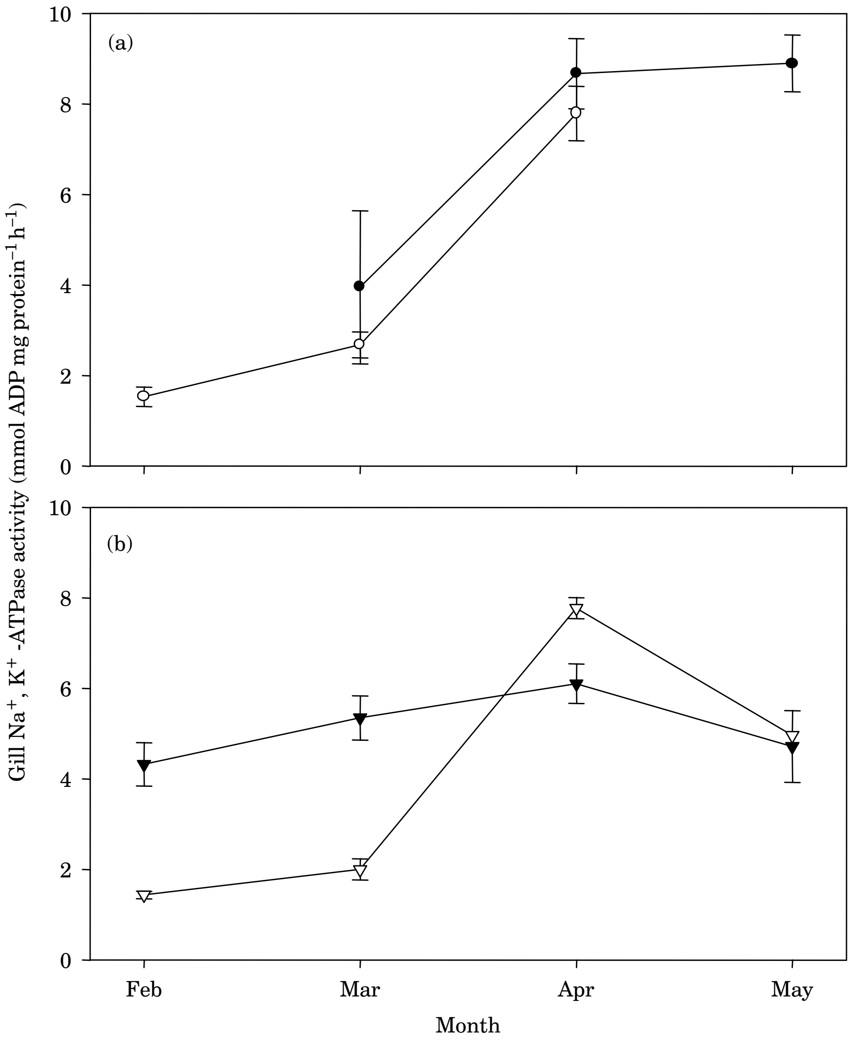

FIG. 5. Gill Na^+, K^+ -ATPase activity levels for juvenile (a) hatchery (○) and wild (●) coho salmon and (b) hatchery (▽) and wild (▼) steelhead. Data are from wild smolts sampled in the trap net and estuary and hatchery fish sampled at the hatchery in February and March 2003 and in the trap during April and May 2003.

migration did not begin until April, no migrating wild coho salmon of sufficient size could be sampled in February, and only two were sampled in March. In addition, no samples were collected from hatchery coho salmon in May, because they were no longer present. Wild coho ATPase activity did not differ significantly among March ($n = 2$), April ($n = 22$) and May ($n = 17$, $P = 0{\cdot}127$). Hatchery coho salmon ATPase activity, however, rose significantly between March ($n = 24$) and April ($n = 12$, $P < 0{\cdot}001$). Wild coho salmon did not differ from hatchery fish during March ($P = 0{\cdot}895$) or April ($P = 0{\cdot}776$).

The ATPase activity levels of hatchery steelhead were low during February ($n = 11$) and March 2003 ($n = 22$) just before release [Fig. 5(b)]. After March, hatchery fish showed significantly elevated ATPase activity when sampled during their downstream migration in April ($n = 4$, $P < 0{\cdot}001$). Activity levels of the two hatchery steelhead sampled in May ($n = 2$) had declined to an intermediate level between March and April and were not significantly different from either month. The ATPase activity for wild steelhead migrants during February ($n = 12$) and March 2003 ($n = 2$) was significantly higher than levels for hatchery fish during those months (February, $P = 0{\cdot}001$; March, $P < 0{\cdot}001$). Wild steelhead migrating downstream in April ($n = 17$) and May ($n = 10$) did not differ significantly in ATPase activity from hatchery steelhead during that period. The ATPase activity of wild steelhead rose from February to April and then declined in May, but did not differ significantly throughout this time. It should be noted that the hatchery fish were 1 year old at the time of sampling, whereas many of the wild fish sampled in the estuary and downstream migrant trap were 1 to 3 years old.

ADULT STEELHEAD

Age

Adult steelhead scales were analysed to determine total age and the number of years spent in fresh and salt water (Table III). Groups were compared by ANOVA. On the basis of back-calculated size at ocean entry, no significant differences in juvenile age were observed between sexes in time spent in fresh water ($P = 0{\cdot}214$). Hatchery fish departed from fresh water at a younger age than wild fish ($P < 0{\cdot}001$). In terms of time spent in salt water, no differences between hatchery and wild fish were observed ($P = 0{\cdot}131$). Males, however, spent less time at sea than females ($P = 0{\cdot}018$). Finally, there were no significant differences for age-at-return between hatchery and wild fish ($P = 0{\cdot}353$) or between the sexes ($P = 0{\cdot}195$).

TABLE III. Total age, time in fresh and salt water as determined by scale analysis for hatchery and wild steelhead

	Freshwater age (years)		Saltwater age (years)		Total age (years)	
	n	Mean ± s.e.	*n*	Mean ± s.e.	*n*	Mean ± s.e.
Hatchery males	10	1·30 ± 0·15	10	1·90 ± 0·10	10	3·20 ± 0·13
Hatchery females	23	1·22 ± 0·09	23	2·17 ± 0·18	23	3·39 ± 0·18
Wild males	23	1·78 ± 0·09	23	1·54 ± 0·12	23	3·33 ± 0·13
Wild females	22	1·59 ± 0·11	23	2·04 ± 0·13	22	3·59 ± 0·16

	Hatchery *v.* wild			Male *v.* female	
	n	*F*	*P*	*F*	*P*
Freshwater age	78	15·309	0·000	1·572	0·214
Saltwater age	79	2·33	0·131	5·886	0·018
Total age	78	0·873	0·353	1·712	0·195

Size of returning adults

The size of returning adult steelhead, captured in 2002–2004, was compared for differences between sexes and between hatchery and wild fish (Fig. 6). The mean ± S.E. L_F for all adult steelhead sampled between 2002 and 2004 was 64·23 ± 0·42 cm. No significant differences were observed in size between any of the groups compared (Kruskal–Wallis test statistic, $n = 491$, $P = 0{\cdot}459$ assuming χ^2 distribution with 3 d.f.). There was no variance in L_F between hatchery and wild males ($F_{61,139}$, $P > 0{\cdot}05$). There was no variance in L_F between hatchery and wild females ($F_{96,195}$, $P > 0{\cdot}05$).

Timing of return

Collection techniques did not discriminate between hatchery and wild steelhead and made it possible to compare relative numbers from each group caught throughout the spawning season. Data on the number of fish caught from the 2002 and 2003 spawning seasons were combined and grouped by month (Fig. 7). There was a significant difference in the timing of return for hatchery *v.* wild fish (χ^2, $n = 140$,

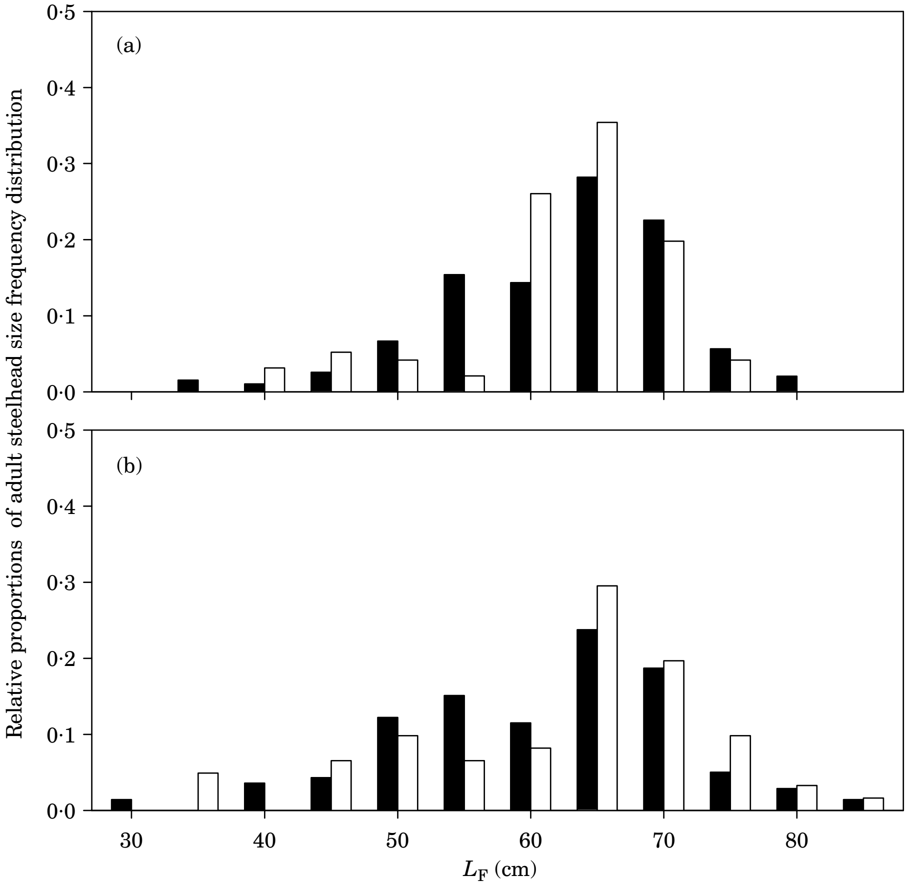

FIG. 6. Histograms of size distribution for (a) hatchery (□, $n = 96$) and wild (■, $n = 195$) female adult steelhead and (b) hatchery (□, $n = 61$) and wild (■, $n = 139$) male adult steelhead caught in 2002, 2003 and 2004.

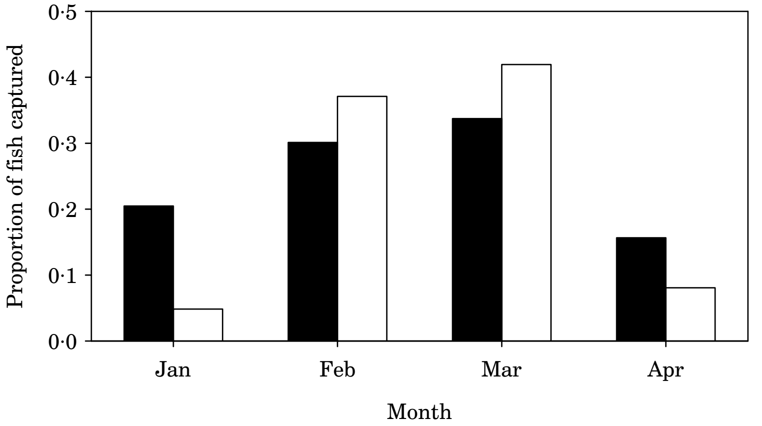

FIG. 7. Proportions of wild (■, $n = 83$) and hatchery (□, $n = 62$) steelhead caught in Scott Creek watershed by month during the spawning season (combined data for 2002 and 2003).

d.f. = 3 $P = 0{\cdot}029$): hatchery fish were more likely to return during the middle of the spawning season and less likely during the beginning and end of the season.

Stream region of return

The data were examined to determine if a disproportionate number of hatchery steelhead returned to Big Creek, the tributary where the hatchery is located, despite having been planted at several locations throughout the watershed (Fig. 1). The hatchery receives its water directly from Big Creek and Berry Creek (a small Big Creek tributary). The proportion of hatchery to wild fish sampled in Big Creek was compared to the proportion of hatchery and wild fish sampled along the main stem of Scott Creek, upstream of the Big Creek tributary confluence. A higher proportion of hatchery fish were captured in Big Creek (38 hatchery to 25 wild) compared to the upper watershed (eight hatchery to 31 wild) (χ^2, d.f. = 1, $P < 0{\cdot}001$), indicating that they preferentially return to the tributary on which the hatchery is located.

Sex ratio

Return data for 2002, 2003 and 2004 were analysed for differences in sex ratio between hatchery and wild steelhead. Skewed sex ratios were observed for both hatchery and wild fish with more females than males in both groups (wild fish, 1·42 : 1, females : male, $n = 336$, χ^2, d.f. = 1, $P = 0{\cdot}002$; hatchery fish, 1·55 : 1, $n = 158$, χ^2, d.f. = 1, $P = 0{\cdot}007$).

Spawning interactions

Steelhead spawner surveys ($n = 69$) were conducted in Big Creek during the spawning seasons of 2002 and 2003 (January to April) and in the early part of 2004. No spawning was observed during 34 of the surveys. Forty-nine spawning events were observed during 35 of the surveys. The dominant male was the largest male present in all cases where competition with a satellite male was observed. Hatchery and wild fish spawned with each other regardless of origin (Table IV). Several times wild male steelhead were observed competing for access to females. There were no confirmed observations of a hatchery male

TABLE IV. Steelhead spawning matrix reporting the number of observations of pair-wise combinations of female-dominant male pairings and dominant males spawning with satellite male present

Dominant male	Wild male	Hatchery male	Unknown male	Mature male parr
Females paired with dominant male				
Wild female	6	10	1	1
Hatchery female	12	5	1	0
Unknown female	4	1	8	0
Satellite males competing with dominant male				
Wild male	5	0	0	0
Hatchery male	2	1	0	0
Unknown male	2	1	2	0
Mature male parr	5	3	2	1

being dominant over a wild male, and only a few observations of hatchery males competing for access to females all. At least one, if not several mature male parr were observed at many spawning events competing with dominant males. Mature male parr were difficult to observe because of their small size; there were probably more of them than were actually seen. There were no observations of female competition for mates, and it is more likely that female competition would be for access to the spawning substratum.

DISCUSSION

Current hatchery practices of raising juveniles to smolt size before release appear to eliminate problems of hatchery fishes preying upon or competing with wild juveniles in the Scott Creek watershed. The ATPase activity levels observed in this study were similar for both hatchery and wild smolts, indicating that all migrating fishes were physiologically prepared to enter salt water regardless of origin. The successful smoltification of the hatchery fishes is attributed to the 'natural' conditions under which they are raised. The hatchery takes in water directly from the stream, creating temperature conditions similar to those experienced by wild fishes. The absence of artificial lighting provides hatchery fishes with a natural photoperiod, which is known to be important to the smoltification process (Thorarensen *et al.*, 1989; Ewing *et al.*, 1995). The hatchery releases smolts in relatively low numbers, approximately equal to the number of wild migrating smolts. Hatchery smolts of both species were larger on average than the migrating wild smolts. But data from the downstream migrant trap and stream surveys indicate that almost all hatchery fishes went to sea soon after planting, leaving little time for them to prey upon or compete with wild fishes. In contrast, the release of hatchery pre-smolt coho salmon into Oregon coastal streams reduces wild pre-smolt abundance partly because of the high densities at which the hatchery fish are planted and the extended time and resources they require to reach the smolt stage (Nickelson *et al.*, 1986).

In this watershed, the low potential for predation or competition between hatchery and wild fishes also results from the short migration distances (<15 km). Other studies that have demonstrated negative effects of artificial propagation on wild stocks have focused on large river systems with migration distances on the order of several hundred kilometres (Flagg *et al.*, 1995, 2000; McMichael *et al.*, 2000; Levin & Williams, 2002). The release of large, ocean-ready smolts may not be effective in systems where hatchery fishes must migrate hundreds of kilometres. Releasing hatchery smolts in the lower sections of large river systems would reduce juvenile hatchery and wild competition and potentially increase adult returns (Solazzi *et al.*, 1991), but would increase the probability of straying (Candy & Beacham, 2000) and the subsequent introgression of hatchery-favoured genetic traits in wild stocks, which may reduce their fitness (Grant, 1997; Unwin & Glova, 1997; Ford, 2002; McLean *et al.*, 2003). While the release of smolts into short coastal basins may reduce negative effects on local wild populations, this strategy does not always work; other management practices (*i.e.* number of fish released and broodstock selected) should be considered simultaneously (Nickelson, 2003).

Hatchery coho salmon and steelhead smolts entered the ocean at 1+ years and spent very little time in the stream. Wild coho salmon also migrated to sea during the same time at 1+ years. Wild steelhead, however, often required ≥2 years before attaining sufficient size to go to sea. From a management perspective, there is no reason to be concerned about this difference, since ultimately the two groups of returning adults were of similar age, and genetic mixing between year classes occurs regularly due to the iteroparous nature of steelhead.

Minor differences in timing were observed between returning wild and hatchery adult steelhead. A more peaked distribution in hatchery return rates was attributed to the more uniform environment, growth conditions and planting date of the hatchery fish, but they returned in phase with wild fish, indicating that the practice of collecting wild broodstock throughout the spawning season is effective. This is in sharp contrast to other systems, where hatchery fishes have been accidentally or intentionally selected to return out of phase with wild stocks either because hatcheries often collect the first fishes to return (Nickelson *et al.*, 1986; Flagg *et al.*, 1995) or because the hatchery stock is not native to the river and has a different run time (Mackey *et al.*, 2001). Historic supplementation practices in Washington used different stocks that returned at different times to avoid crossbreeding of stocks. This is not an option in Scott Creek because ESA regulations preclude interbasin supplementations. Selecting fishes to return out of phase with wild fishes would be a poor management choice, because of the narrow weather window during which southern populations of winter-run fishes have to access the stream. Steelhead and coho salmon runs overlap to a certain degree in central California. Both species' runs begin with the opening of the stream, typically in late December. But coho salmon numbers peak first in January and the run ends in February, whereas the peak steelhead return is late February to March (Shapovalov & Taft, 1954), lasting into April. Any effort to shift run times could increase the probability that the stream would not be open to returning spawners or would increase interspecific competition, potentially harming both species (Levin & Williams, 2002).

Size differences in returning adults can affect fecundity: larger females produce more eggs (Beacham & Murray, 1993), and larger males are more successful in dominance interactions (Fleming & Gross, 1994; Quinn & Foote, 1994). There is concern that hatcheries are selecting the largest returning fishes to enhance fishing and create fishes larger than the wild stock. Neither the mean size, nor variance in size distribution of returning adult steelhead differed between wild and hatchery fish. Contrary to this study, Mackey *et al.* (2001) observed both wild male and female steelhead to be larger than hatchery fish in Forks Creek, WA. They suggested that wild females would be expected to have higher fecundity because larger size translates into increased egg production.

Although surprisingly little is known about steelhead reproductive strategies, it is well established that some steelhead males can become reproductively mature prior to ocean entry (Needham & Taft, 1934; Shapovalov & Taft, 1954; R.G. Titus, D.C. Erman & W.M. Snider, pers. comm.). It is not clear if these males are mature parr that will eventually go to sea or remain instream as resident rainbow trout. One study of downstream-migrating steelhead reported skewed sex ratios among wild smolts, with wild females outnumbering wild males by two to one, whereas hatchery smolts were observed in a one-to-one sex ratio (Titus *et al.*, 2003). This led to a concern that if a large percentage of wild males chose not to go to sea, a disproportionate number of hatchery males relative to wild males would return as anadromous adults. Similar skewed sex ratios, however, were observed for both hatchery and wild steelhead in Scott Creek. The reason for the skewed sex ratio in hatchery fish requires further investigation.

Observations of steelhead spawning indicate that hatchery and wild fish interbreed regularly. During spawning interactions, the largest male always held the dominant position behind females, regardless of origin. This finding is consistent with previous studies indicating that male size is related to female mating choice in Pacific salmonids (Berejikian *et al.*, 2000). Hatchery males were rarely observed competing with wild males in this study and may be competitively inferior, avoiding conflict with wild males. This has been observed in studies of coho salmon where wild males outcompeted both hatchery males and captively reared males, and both wild and captively reared females attacked captively reared males more frequently (Fleming & Gross, 1992; Berejikian *et al.*, 1997, 2001).

No direct competition between female steelhead for access to spawning sites was observed, but, both hatchery and wild females were observed spawning at many of the same sites at different times. Superimposition of redds did occur on a few occasions, but seemed to be a natural part of the steelhead behaviour with no specific hatchery or wild bias. The effect on egg development and emergence is unclear and is probably influenced by environmental conditions as much as fish density. During the winter of 2002, regular mild rains kept the creek mouth open to returning adults throughout the spawning period, during which time superimposition occurred. But in the 2003 winter, heavy rains alternated with several-week dry periods. Fresh 'cohorts' of fry from early spawning periods were often emerging from redds before the next rains enabled a second group of fish to enter the stream, reducing the potential for superimposition. Because only one female was ever observed spawning in a pool at a given time, spawner densities were far lower than observed in north-west Pacific rivers and streams.

This implies that hatchery production is not exceeding the watershed's carrying capacity.

Although the hatchery plants smolts throughout the watershed, more hatchery fishes return to the Big Creek tributary where the hatchery is found. Thus any effects on wild stocks are most likely to be observed or exacerbated in the Big Creek tributary. A solution may be to plant fishes in all tributaries except Big Creek and assume that a certain number will stray there regardless of where they are planted. The homing instinct of steelhead stocks from other local river basins (*i.e.* San Lorenzo River, 25 km south of Scott Creek mouth) raised at Big Creek hatchery must be considered. Fishes raised in Scott Creek waters (at the hatchery on Big Creek) to the smolt stage and planted in other rivers may not spend enough time in their planted stream to imprint and return. Although the hatchery has data to show that these fish do in fact return in large numbers to their native river, it is possible that there is an artificially high straying rate to Scott Creek where the fishes were raised. Planting fishes at younger ages in their true stream of origin might enhance their imprinting abilities and reduce straying. Planting juveniles during the parr stage, however, may result in greater hatchery and wild competition in the juvenile stages, which is presently being avoided. One compromise would be to transfer fishes to satellite rearing facilities on their native streams during the parr stage or, alternatively, to identify stream sections for planting hatchery parr where wild populations are weak or non-existent relative to the carrying capacity (Nickelson *et al.*, 1986).

This is one of the first efforts to evaluate the effects of artificial propagation in a watershed where conservation hatchery strategies are being employed. Additional research is required in the areas of relative reproductive success of hatchery and wild fishes, escapement, population genetics and long-term population trends. It does appear, however, that many of the classical problems associated with juvenile competition and artificial selection affecting adult return times, size and spawning behaviour are being avoided. The conclusions of this study are that conservation hatchery strategies can be effective in small watersheds and that, whenever possible, supplementation efforts should focus on quality of production efforts rather than quantity of fishes produced in order to ensure the health of wild salmonid populations.

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