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[Article]

Behavior and Survival of Wild and Hatchery-Origin Winter Steelhead Spawners Caught and Released in a Recreational Fishery

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Abstract.—Mandatory catch and release of wild fish and supplementation with hatchery-reared fish are commonly used to sustain sport fisheries on low-abundance populations of wild steelhead. However, their effectiveness in limiting angling mortality on wild fish is uncertain. We radio-tagged 226 (125 wild, 101 hatchery) angled adult steelhead *Oncorhynchus mykiss* near the mouth of the Vedder−Chilliwack River, British Columbia, in 1999 and 2000 and monitored their subsequent movements to determine survival to spawning and overlap in the distributions of inferred holding sites, spawning sites, and spawning times. The distributions of prespawning holding sites did not differ between wild and hatchery fish in either year, but spawning locations differed. Holding and spawning sites used by hatchery fish were restricted to the lower two-thirds of the river, downstream of the hatchery where they were reared but well upstream of their smolt release site. Wild fish spawned throughout the watershed. Spawning times did not differ between wild and hatchery fish, but varied with run timing. The maximum mortality from the initial catch and release and radio-tagging was 1.4% in 1999 and 5.8% in 2000; true mortality rates were lower because tag regurgitation was indistinguishable from death. The fishery subsequently killed 2.5% of tagged wild fish and harvested 20% (1999) and 43% (2000) of the hatchery fish. Seventy-two tagged fish were recaptured and released in the sport fishery up to three times without any mortality before spawning. Hatchery fish were recaptured at twice the rate of wild fish. At least 92% of unharvested fish spawned, and 75% of successful spawners survived to emigrate from the watershed. The incidence of postspawning death did not vary with the frequency of capture and release. Catch-and-release angling imposed small costs in terms of survival; however, behavioral differences existed between adult wild fish and the adult F_1 progeny of wild fish reared to smolt stage in a hatchery.

Open-access sport fisheries that target small populations of a highly desired species challenge the ability of regulators to maintain viable fish populations while sustaining popular and economically important fisheries. Recreational fisheries for winter-run steelhead *Oncorhynchus mykiss* provide examples of such a situation. Winter-run steelhead returning to their natal rivers to spawn support important recreational fisheries along the Pacific coast of North America (Pauley et al. 1986; Smith et al. 2000). Several characteristics make wild steelhead stocks susceptible to overharvest by sport fisheries: spawner numbers are often very low (e.g., Ward 2000); spawners may hold in-river, where they are vulnerable to capture, for long periods before spawning; and they are eagerly sought by anglers because of their aggressiveness, large size, and beauty.

There are essentially two options available to fishery managers to maintain sustainable sport fisheries for steelhead: limit mortality or increase spawner abundance. Fishing mortality may be controlled by limiting angler effort with time and area closures; reducing catchability via gear restrictions; and reducing the kill via gear restrictions, harvest quotas, and catch-and-release regulations. Catch-and-release regulations are a particularly

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desirable management option because they may obviate other restrictive regulations if postrelease survival to spawning is sufficiently high. There are many studies of short-term (typically 24–96 h) mortality following catch and release for salmonids other than steelhead and of factors that influence this immediate mortality (e.g., Taylor and White 1992; Muoneke and Childress 1994; Gjernes et al. 1993; Lindsay et al. 2004), but there are few studies of survival to spawning (Bendock and Alexandersdottir 1993; Webb 1998). The effect of multiple captures on survival is uncertain. Because the physiological cost of sexual maturation and spawning is high in steelhead, many nonangled fish do not survive (Ward and Slaney 1988). The additional physiological stress from catch and release may further reduce either survival to spawning or postspawning survival to the time of emigration from the natal stream to the ocean.

Spawner abundance may be increased by increasing smolt production through manipulations of the physical habitat used by wild fish during the egg incubation and juvenile stream-rearing stages (i.e., habitat rehabilitation) or through hatchery programs that rear and release juveniles. Hatchery programs are common but may have unintended adverse impacts on the demography or fitness of small populations of wild fish (Skaala et al. 1996; Unwin and Glova 1997; Chilcote 2003) if hatchery-produced fish differ from wild fish because of inadvertent selection during hatchery rearing (Glover et al. 2004; Kostow 2004) or if domesticated or nonnative brood stocks are used (McLean et al. 2003). Abundant hatchery fish may also result in unsustainable mortality rates on a less productive wild stock, where both are removed by a common fishery. To reduce potential differences between wild and hatchery-produced fish, hatchery programs may use wild fish as broodstock and employ rigorous mating protocols to maintain genetic diversity, particularly when hatchery fish are intended to supplement the naturally breeding population. Both conventional hatchery programs and supplementation programs remain controversial because of uncertainties about the impacts of hatchery fish on wild fish production (ISAB 2003; Brannon et al. 2004).

There is little information on behavioral differences between wild and hatchery-origin steelhead spawners, such as the location and timing of holding sites and spawning activities, which mediate interactions between the two groups and with the fishery. Differences in timing and distribution may allow managers to direct fishing mortality away from low-abundance wild fish (Ludwig 1995; Mackey et al. 2001). Overlap in the timing and distribution of spawning could allow adverse ecological interactions or undesired interbreeding between hatchery-origin and wild steelhead (Leider et al. 1984).

We used radiotelemetry to (1) determine the in-river spatial distributions of wild and hatchery-origin winter steelhead spawners that were exploited in a recreational fishery and (2) measure the survival of wild and hatchery adults from the time of capture in the sport fishery shortly after river entry to the time of postspawning emigration from the river. We compared the spatial distribution of prespawning holding sites and the timing and distribution of spawning for wild and hatchery fish. We also compared survival rates to assess the utility of catch-and-release regulations in maintaining the abundance of wild spawners.

Study Site

The study was conducted in the Vedder–Chilliwack River of southwestern British Columbia, a fifth-order stream that enters the lower Fraser River about 95 km upstream from the ocean (Figure 1). The watershed is large (1,230 km^2), mountainous, and mostly forested, but agricultural lowlands surround the lowermost 15 km of the river, a portion of which has been channelized. Roads occur in close proximity to the channel throughout the entire watershed. Maher and Larkin (1954) document the life histories of Chilliwack River steelhead. Winter-run steelhead enter the river from November to May and spawn throughout the system as far upstream as tributaries to Chilliwack Lake, 61 km upriver. A hatchery located at river kilometer (rkm) 38.5 has produced about 128,000 (1992–2002 average) age-1 smolts annually from 1982 onward. Hatchery smolts are the F_1 progeny of randomized crossings of about 36 male and 36 female wild steelhead adults taken from the river each year. All hatchery smolts are adipose-clipped to distinguish them from naturally spawning fish. Smolts are released in the main stem of the river below rkm 16.

The winter steelhead sport fishery, which is is restricted to the area downstream of the hatchery, yields about 48,000 angler-days of effort annually (1992–2002 average; G. A. Wilson, British Columbia Ministry of Water, Land, and Air Protection, personal communication) between late November and April. The fishery is closed between 1 May and 30 June, except for a fly-fishing-only zone below Vedder Crossing (rkm 16.5) that is

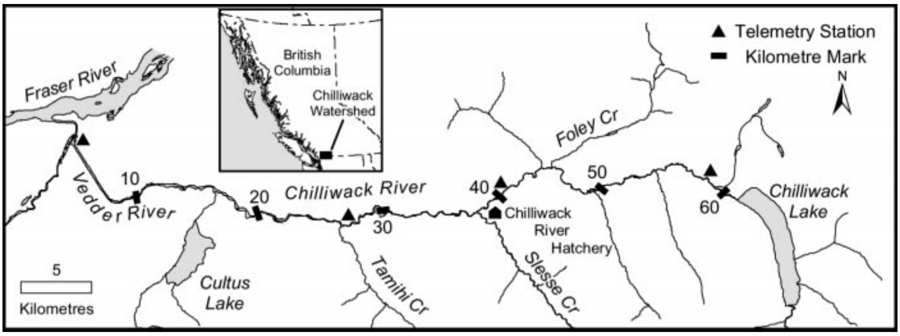

FIGURE 1.—Map of the Vedder−Chilliwack River watershed, British Columbia, showing the locations of the fixed telemetry stations used to detect radio-tagged steelhead. Note that the name of the river changes near river kilometer 16.

open during May. The fishery is primarily a bait fishery using salmon roe or ghost shrimp *Callianassa calliforniensis* on conventional J-shaped, barbless, single hooks drifted along the bottom. Wild steelhead (i.e., those with an intact adipose fin) must be released unharmed. Anglers may retain one hatchery steelhead daily, but about 55% (1992–2002 average) of the angled hatchery fish are released. The ratio of wild to hatchery fish in the reported catch is about 1.8:1 (9,800 wild to 5,600 hatchery fish; 1992–2002 average). Surveys indicate much lower total spawner abundances than the reported catches (Lill 2002), which suggests that many fish are caught multiple times.

Methods

We radio-tagged and released 72 angled steelhead (31 hatchery, 41 wild) between 5 January and 11 May 1999 (1999 study year) and 154 steelhead (70 hatchery, 84 wild) between 23 December 1999 and 30 April 2000 (2000 study year). We attempted to tag equal numbers of fish within groupings (female, male; hatchery, wild) each month to compare the behavior of different timing components of the run. About 75% of the fish were tagged in the lower 15 rkm. Most fish (89%) were caught by recreational anglers, and the rest were angled by project technicians. Seventy percent were caught on bait, with the remainder caught on coloured yarn. Most fish (91%) were fresh-run (i.e., silver colored). Two fish were rejected because of large natural wounds (open bites), but otherwise fish were tagged regardless of condition. None, however, had angler-caused wounds other than bleeding (five fish). When an angler was observed playing a fish, a project technician asked whether the angler intended to retain or release the fish and whether a fish intended for release could be tagged. Fish were landed normally. Once landed, fish to be tagged were held in a cylindrical, dark fabric, holding tube. Fish were identified as wild or hatchery-origin by the presence or absence of the adipose fin, sexed, and measured (fork length, cm); then a Lotek Engineering (Newmarket, Ontario) Model MCFT-3A or Model CFRT-7A radio transmitter was inserted into the stomach via the mouth. The 40-cm antenna exited the mouth and trailed back along the body. Each radio tag had a unique frequency and numeric code combination. All fish were also tagged dorsally with a uniquely numbered, coloured spaghetti tag (Floy Tag Inc., Seattle). Fish were not anesthetized during tagging. Tagged fish were usually held for 3–5 min to allow recovery from handling stress. A few fish were held for longer periods until they began swimming strongly. Water temperatures were low (4–7°C).

We established four fixed-station receiver sites (Figure 1) that operated continuously until early July in each study year. The Lotek Model SRX-400 receivers had two directional antennae, one oriented upstream and one downstream. We tested signal directionality by placing a transmitting radio tag upstream or downstream and noting signal strengths at known distances. Gain on the receivers was reduced to a give a range of about 200 m in either direction, which allowed passage of fish to be determined. Data were downloaded at 5-d to 7-d intervals. We conducted mobile surveys by vehicle and by foot along the entire main-stem river downstream of Chilliwack Lake, usually on the same day as the fixed-station downloads. In 2000 we also surveyed the lower reaches of several major tributaries (Foley, Slesse, Tamihi creeks). In addition to the regular mobile surveys, we surveyed the river by helicopter twice in 1999 (February and April), and we surveyed the upper river by raft on three occasions in 2000 (February and March). During mobile surveys we used a handheld, H-shaped antenna (Lotek Model AN-ADH) connected to a SRX-400 receiver. Individual fish were identified from their unique signal frequency and pulse rate combinations. Signal strength was used to determine fish location to within 250 m or less by reference to known landmarks.

Some radio-tagged fish were recaptured in the sport fishery. We obtained information on the spaghetti-tag or radio-tag number, location, and date of recaptures through voluntary reporting by anglers. To encourage reporting, we advertised the study widely, established toll-free telephone reporting, and awarded project hats and established prize draws for anglers who provided data. The active participation of local angling organizations and retailers greatly aided data acquisition. When a radio-tagged hatchery fish was killed by an angler, we obtained the tags and reused the radio transmitter (4 fish in 1999, 24 fish in 2000). Although we believe that reporting rates were high, we know that some recaptures were not recorded. We found one unreported radio tag on shore. We believe that seven other radio-tagged fish (six hatchery, one wild) were killed but not reported because fish with multiple detections abruptly vanished from popular fishing sites. We treated these as angler-killed fish in our analyses. The fates of six angler-recaptured fish (one hatchery, five wild; all males) cannot be determined because the radio transmitter was removed by the angler before release, although the data were reported.

We inferred the behavior of tagged fish from changes in the location of tag detections through time (Figure 2). We assumed that a stationary tag location near the release site indicated fish death that was attributable to tagging, although tag regurgitation (Keefer et al. 2004) was also possible; sustained upstream movement, particularly through a site with rapid water velocity, indicated posttagging survival. We expected upstream movement to potential spawning sites to be saltatory—that is, fish would hold at particular sites for variable periods that might depend on environmental conditions, such as temperature, photoperiod, or discharge (Webb 1998). We identified holding sites as locations where fish remained stationary for extended periods, after which they moved upstream (Figure 2). Often a holding site could be associated with a pool or a middepth run that provided cover. We identified spawning sites and times from a rapid, relatively short-duration upstream movement to a location suitable for spawning (where this was assessable), followed by either rapid downstream movement or by a stationary tag, which we took to indicate death. In cases where distinct upstream movement from a holding site was not evident (e.g., because spawning sites were near holding sites), area-restricted movement at a site suitable for spawning followed by rapid downstream movement was assumed to indicate a spawning location (Burger et al. 1985). Because fish were not observed directly and were not tracked continuously, our ability to identify holding and spawning sites depended in part on the number and temporal resolution of the relocations of individuals: some imprecision in the determination of these locations

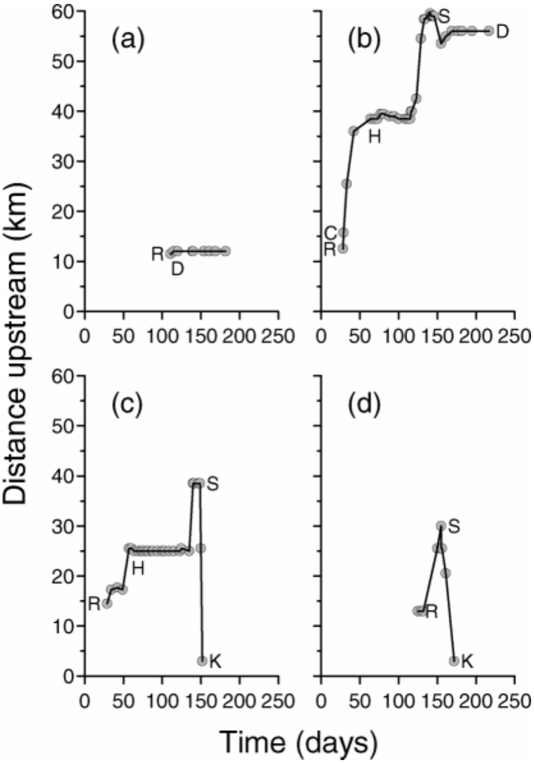

FIGURE 2.—Time versus location (river kilometers upstream) plots for selected radio-tagged steelhead in the Vedder−Chilliwack River, British Columbia, illustrating how the location or timing of particular events (holding, spawning, emigration, or death) was inferred from the tag detection data. Panel **(a)** indicates tagging and release (R) and abrupt death or tag regurgitation following tagging (D). Panel **(b)** indicates R, capture and release by an angler (C), prespawning holding (H), spawning (S), and D. Panel **(c)** indicates R, H, S, and emigration (kelting [K]). Panel **(d)** indicates R, S, and K without prespawning holding. Time is measured from 1 December 1999.

is inevitable. We identified as kelts those fish that subsequently migrated downstream past the receiver station near the river mouth. The timing of emigration (''kelting'') was the date at which a fish passed the lowermost receiver site moving in a downstream direction.

We used the Kolmogorov–Smirnov two-sample test (KS) to compare the spatial distributions of holding or spawning sites between wild and hatchery fish. We used the KS test because the data were nonnormally distributed and because the test is sensitive to differences in dispersion, skewness, and location (Sokal and Rohlf 1981). We first compared the distributions of male and female fish of the same origin in the same year. Where the distributions did not differ, we pooled sexes in comparing distributions between fish types in a given year. We used analysis of variance (ANOVA) to assess differences in the timing of spawning or emigration within each year. Fish origin (wild or hatchery), fish sex, and run-timing group (early = December and January tagging, middle = February and March, late = April and May), were treated as fixed factors in a three-way factorial design. We used Levene's test to assess homogeneity of variances, and we transformed data to stabilize variances where necessary. We used Tukey's test to contrast the means of factors that differed at $\alpha = 0.05$. We tested differences in the time interval between tagging and spawning among run-timing groups within each year with a Kruksal–Wallis one-way ANOVA (KW) because common transformations did not stabilize the variances. We used one-way ANOVA and Tukey's test to compare the mean size of radio-tagged fish within origin and sex groups each year.

We compared the proportions of unharvested fish that survived to spawn between the hatchery and wild fish categories and between the female and male categories using three-way contingency table analysis based on log-linear models (Sokal and Rohlf 1981) in which terms were tested by individually deleting them from the model and comparing the fit against the saturated model. Significant interaction terms indicated differences in survival between the elements of the categories. We compared the proportions of spawning fish that survived to the kelt stage in the same way. We used Bonferroni-adjusted significance levels to maintain $\alpha = 0.05$ for multiple models. In calculating survival proportions, we have treated all stationary tags as mortality, although some may be tag regurgitation. Where contingency analysis indicated no differences in survival between groups, we pooled data over groups to estimate the proportions surviving. We used binomial 95% confidence intervals (CI) to represent the uncertainty in survival proportions. We used Pearson's χ^2 to compare survivals among fish caught and released different numbers of times, and we pooled the data from fish recaptured two and more times to avoid low cell frequencies.

Results

Radio-tagged steelhead averaged 73 cm in fork length (range: 56–99 cm). Within years, wild fish were slightly larger than hatchery fish (Table 1). The mean size of wild males in 1999 was about 6 cm greater than either hatchery fish or wild females (ANOVA: $F_{3,68} = 4.51$, $P = 0.006$), whereas the mean size of wild females in 2000 was about 4 cm larger than hatchery fish (ANOVA: $F_{3,\ 150} = 4.57$, $P = 0.004$). The ratio of wild to hatchery fish tagged was 1.32:1 in 1999 and 1.20:1 in 2000. Females outnumbered males in both years (1.40:1 in 1999 and 1.96:1 in 2000).

The prespawning holding sites used by hatchery fish were restricted to the area downstream of rkm 42 in both years (Figure 3), sites between rkm 10 and rkm 16 and between rkm 32 and rkm 39 being most frequently used. The distributions of holding sites used by wild fish did not differ from those used by hatchery fish (1999: KS = 0.206, $P = 0.49$; 2000: KS = 0.253, $P = 0.60$), although some wild fish held at sites upstream of rkm 40 during 1999. Spawning sites used by hatchery fish were clustered in the middle reach of the river immediately downstream of the hatchery, whereas spawning sites used by wild fish were more broadly distributed (Figure 4). Half of the wild fish spawned in reaches upstream of locations used by hatchery-origin spawners. The distributions of spawning sites differed significantly between hatchery and wild fish in both years (1999: KS = 0.448, $P = 0.007$; 2000: KS = 0.544, $P < 0.001$).

The mean date of the start of spawning activity did not vary between hatchery and wild fish in either year (ANOVA for 1999: $F_{1,43} = 0.38$, $P = 0.53$; for 2000: $F_{1,93} = 0.24$, $P = 0.63$) but did vary significantly among run components (Figure 5), early-run fish spawning about 20 d before late-run fish (Tukey's test: $P < 0.003$ for 1999, $P < 0.007$ for 2000). The interval between tagging and the inferred start of spawning varied among run-timing groups in each year (1999: KW = 26.6, df = 2, $P < 0.001$; 2000: KW = 70.7, df = 2, $P < 0.001$), early-run fish holding for much longer periods before spawning (Figure 6). Most fish moved

TABLE 1.—Numbers, mean ± SE fork length, and fate of radio-tagged steelhead spawners in the Vedder–Chilliwack River, British Columbia, by origin (hatchery or wild) and sex in 1999 and 2000.

Fate, number tagged, and length	Hatchery		Wild	
	Females	Males	Females	Males
		1999		
Died or regurgitated tag	0	1	0	0
Killed by angler	1	5	0	1
Spawned and died	2	3	4	7
Spawned and kelted	12	6	22	5
Unknown	0	1	1	1[a]
Total number tagged	15	16	27	14
Fork length (cm)	74.3 ± 1.6	75.4 ± 1.6	75.1 ± 0.9	82.0 ± 2.3
		2000		
Died or regurgitated tag	3	0	3	3
Killed by angler	24	5	0	2
Spawned and died	8	1	6	10
Spawned and kelted	21	8	37	18
Unknown	0	0	0	5[a]
Total number tagged	56	14	46	38
Fork length (cm)	70.0 ± 0.9	68.2 ± 1.3	73.6 ± 0.9	73.4 ± 1.3

[a] Radio tag removed upon recapture by angler and fish released alive.

downstream rapidly after spawning and exited the river (Figure 2). Early-run fish emigrated at an earlier date than middle-run and late-run fish (Figure 7; Tukey's test: $P < 0.048$ for 1999 and $P < 0.015$ for 2000), but the mean date of kelting did not vary between hatchery and wild fish in either year (ANOVA for 1999: $F_{1,36} = 2.81$, $P = 0.10$; for 2000: $F_{1,70} = 2.30$, $P = 0.13$). The duration of spawning and emigration was similar for all fish; the interval between the start of spawning and kelting did not vary among run-timing components (ANOVA for 1999: $F_{2,28} = 1.76$, $P = 0.19$; for 2000: $F_{2,68} = 1.72$, $P = 0.18$) or between wild and hatchery fish (ANOVA for 1999: $F_{1,28} = 1.21$, $P = 0.28$; for 2000: $F_{1,68} = 0.039$, $P = 0.84$).

Apart from angler harvest, the postrelease mortality of radio-tagged fish was low (Table 1). The nonharvest mortality was 1.4% (95% CI = 0.03–7.5%) in 1999 and 5.8% (2.7–10.8%) in 2000. Mortality occurred soon after release. In 9 of 10 cases, tags were stationary from the first detection (median interval = 3 d postrelease); six of these occurred at the release site and the others were within 2 km. One fish survived 42 d and moved upstream 10 km before dying. None of the mortalities were bleeding at release. Anglers harvested 20% (CI = 7.7–38.6%) of the hatchery fish in 1999 and 43.3% (31.2–56.0%) in 2000. They also killed 2.4% (CI = 0.06–12.9%) of the wild fish in 1999 and 2.6% (0.3–8.9%) in 2000. Thus, most caught-

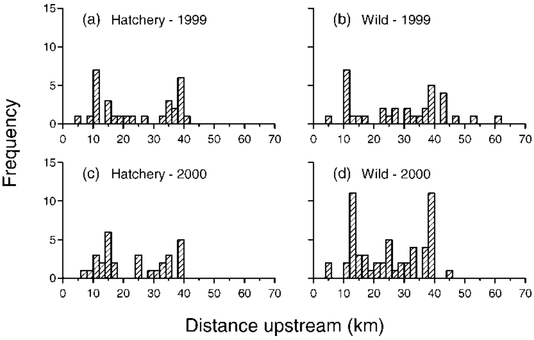

FIGURE 3.—Prespawning holding locations (river kilometers upstream) inferred from plots of location versus time for hatchery versus wild radio-tagged steelhead in the Vedder–Chilliwack River, British Columbia, in **(a)**–**(b)** 1999 and **(c)**–**(d)** 2000. Bar width is 2 km.

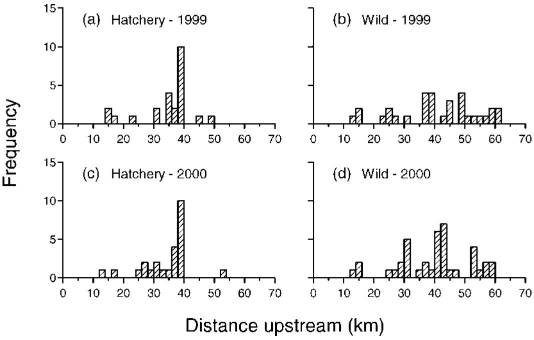

FIGURE 4.—Spawning locations (river kilometers upstream) inferred from plots of location versus time for hatchery versus wild radio-tagged steelhead in the Vedder–Chilliwack River, British Columbia, in **(a)**–**(b)** 1999 and **(c)**–**(d)** 2000. Bar width is 2 km.

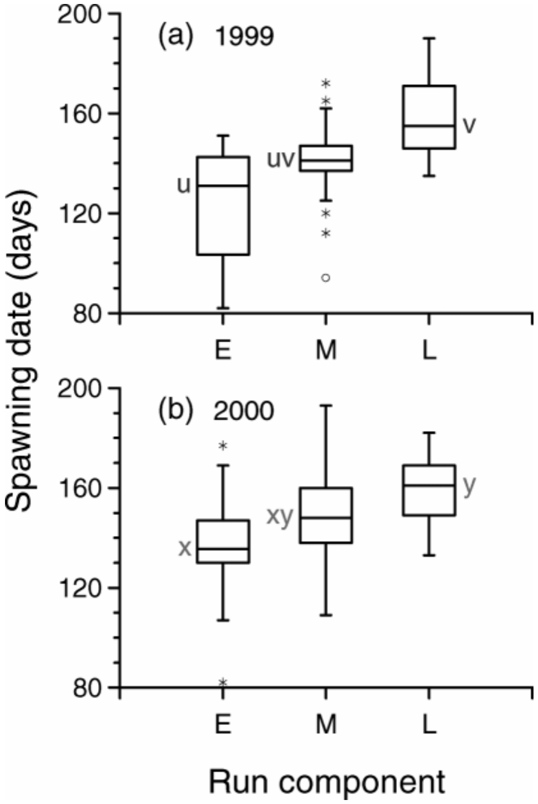

FIGURE 5.—Box-and-whisker plots of inferred spawning dates of radio-tagged steelhead in the Vedder−Chilliwack River, British Columbia, for early- (E), middle- (M), and late-run (L) groups in 1999 and 2000. The horizontal line is the sample median, the box edges are the 25% and 75% quartiles, and the whiskers encompass values within 1.5 times the interquartile range of the edges. Asterisks indicate outliers, and open circles indicate extreme values. Dates are measured from 1 December of the preceding year. The means of groups indexed with different letters within a year (u, v, x, y) differ significantly at $\alpha = 0.05$.

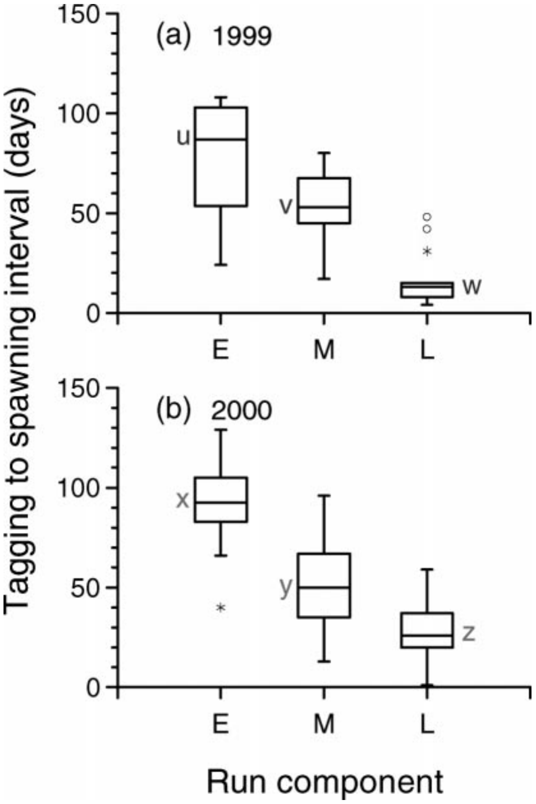

FIGURE 6.—Box-and-whisker plot of the interval between the dates of tagging and spawning for radio-tagged steelhead in the Vedder−Chilliwack Rivers British Columbia, for early- (E), middle- (M), and late-run (L) groups in 1999 and 2000. See Figure 5 for additional information.

and-released wild fish survived to spawn (Table 1). The proportions of unharvested fish that survived to spawn did not differ between wild and hatchery fish or between females and males in either year (Table 2). In 1999, 92.0% (74.0–99.0%) of the hatchery fish remaining after angler harvest and 97.4% (86.5–99.9%) of wild fish remaining after harvest and tag removal by anglers survived to spawn. In 2000, 92.7% (80.1–98.5%) of the hatchery fish and 92.2% (83.8–97.1%) of the wild fish survived to spawn. Similarly, the proportions of successful spawners that survived to kelt did not differ between wild and hatchery origins or between females and males in either year (Table 3). In 1999, 73.8% (60.9–84.2%) of successful spawners kelted; in 2000, 77.1% (68.0–84.6%) of the spawners kelted. Multiple capture and release had no effect on survival to spawning (Table 4) because we observed no prespawning deaths among fish caught and released multiple times. The proportion of successful spawners that died before kelting also did not vary among fish that were recaptured and released different numbers of times (Table 4; $\chi^2 = 0.478$, df = 2, $P = 0.79$). Hatchery steelhead were recaptured at significantly higher rates than wild steelhead (0.45 versus 0.22; $\chi^2 = 18.76$, df = 2, $P < 0.001$).

Both the proportion of tagged fish subsequently recaptured and the proportion killed by anglers differed among run-timing components in 2000 (recaptures: $\chi^2 = 16.46$, df = 2, $P = 0.0003$; angler mortality: $\chi^2 = 8.60$, df = 2, $P = 0.014$), earlier fish having the higher rates of recapture and har-

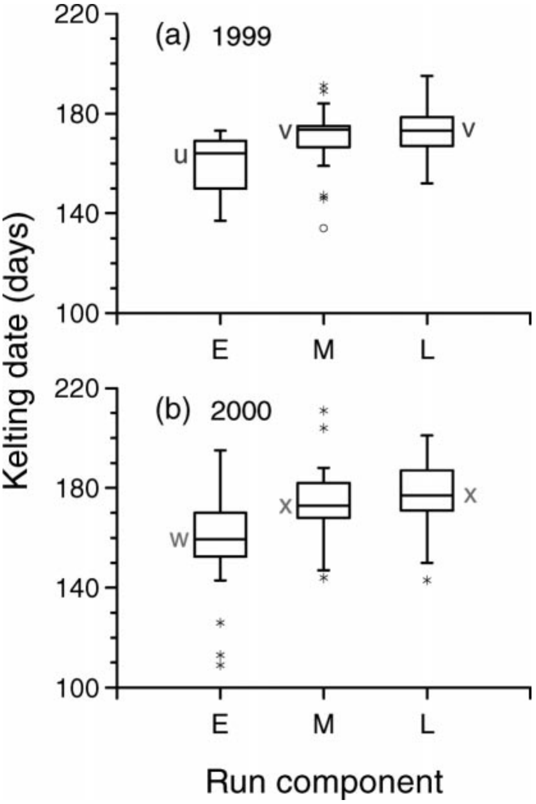

FIGURE 7.—Box-and-whisker plots of dates of emigration (kelting) of radio-tagged steelhead in the Vedder−Chilliwack River, British Columbia, for early- (E), middle- (M), and late-run (L) groups in 1999 and 2000. See Figure 5 for additional information.

vest (Table 5). However, neither the recapture rate nor the harvest rate varied by run-timing component in 1999 (recaptures: χ^2 = 4.77, df = 2, P = 0.09; angler mortality: χ^2 = 0.06, df = 2, P = 0.97), although rates tended to be higher for earlier timing components.

Discussion

Catch-and-release angling for winter steelhead in the Vedder–Chilliwack River in 1999 and 2000 resulted in an average mortality of 3.6% (SE = 2.2%, N = 2) before spawning. There was no difference in the survival to spawning of fish captured and released multiple times or in the subsequent survival from spawning to emigration from the river. An additional 2.5% of wild steelhead was harvested, however, despite nonretention regulations. Because our study lacked a nonangled control group of radio-tagged fish, our estimate of catch-and-release mortality included the effects of tagging and tag loss and, thus, is likely to be biased high. We believe that the catch-and-release mortality estimate of 3.6% included tag loss and tagging-related mortality because (1) most of the inferred deaths occurred at or near the release site shortly after tagging, (2) no deaths were observed among radio-tagged fish known to be recaptured and released by anglers, and (3) survival did not vary with the frequency of recapture. Other studies have found loss rates for intragastric radio tags to be about 4.0% for steelhead (Keefer et al. 2004); rates for other large salmonids have ranged between 2% (Ramstad and Woody 2003) and 16% (Smith et al. 1998). If tag loss in our study was similar to the rates reported elsewhere, then the mortality from catch-and-release angling will be

TABLE 2.—Hierarchical contingency analysis of the number of caught-and-released, radio-tagged wild and hatchery steelhead that survived to spawn in the Vedder–Chilliwack River, British Columbia, in 1999 and 2000. A nonsignificant χ^2 for removal of an interaction term indicates homogeneous proportions across the levels of the factors. The fish origin category compares wild and hatchery steelhead. The survival category compares the number of unharvested fish available to spawn with the number that spawned; survival did not vary between wild and hatchery fish or between males and females in either year.

Factor removed	χ^2 for removal	df	P
1999			
Fish origin × sex × survival category	0.10	1	0.76
Sex × survival category	0.12	2	0.94
Sex × fish origin	1.51	2	0.47
Fish origin × survival category	0.12	2	0.94
2000			
Fish origin × sex × survival category	0.04	1	0.83
Sex × survival category	0.04	2	0.97
Sex × fish origin	6.99	2	0.03
Fish origin × survival category	0.04	2	0.97

TABLE 3.—Hierarchical contingency analysis of the number of spawning caught-and-released, radio-tagged wild and hatchery steelhead that survived to kelt in the Vedder–Chilliwack River, British Columbia, in 1999 and 2000. Refer to Table 2 for details.

Factor removed	χ^2 for removal	df	*P*
1999			
Fish origin × sex × survival category	0.26	1	0.61
Sex × survival category	1.58	2	0.45
Sex × fish origin	1.62	2	0.44
Fish origin × survival category	0.40	2	0.82
2000			
Fish origin × sex × survival category	0.54	1	0.46
Sex × survival category	0.74	2	0.69
Sex × fish origin	3.07	2	0.22
Fish origin × survival category	0.55	2	0.76

considerably lower than the 3.6% estimated for the combined effects of tag loss and catch and release. Although small in magnitude, mortality from catch-and-release angling may nevertheless contribute to the decline of populations with greatly depressed productivity (e.g., by the reductions in smolt-to-adult survival associated with variations in marine productivity; Ward 2000). Because steelhead are iteroparous and repeat spawners may be more fecund or more successful, small increases in adult mortality may cause disproportionate decreases in juvenile production.

Although hooking mortality rates for anadromous salmonids vary widely (Hooton 1987; Bendock and Alexandersdottir 1993; Muoneke and Childress 1994; Webb 1998; Dempson et al. 2002; Thorstad et al. 2003), our mortality estimate is in the lower portion of the reported range. It is, however, similar to mortality rates (2.6%-3.6%) reported by Hooton (1987) for winter steelhead caught on baited, barbless hooks. Mortality rates vary with factors such as hook type (DuBois and Kuklinski 2004) and hooking location (Lindsay et al. 2004), which determine the extent of wounding; mortality rates also vary with temperature (Dempson et al. 2002), air exposure (Ferguson and Tufts 1992), and a fish's physiological state (Brobbel et al. 1996). Several factors may reduce physiological stress and mortality for angled steelhead in our study. First, water temperatures were low (4–7°C); mortality is most commonly associated with water temperatures above about 18°C (Dempson et al. 2002). Second, because catch-and-release regulations for wild steelhead have been in force in the Chilliwack River since 1985, most successful anglers are familiar with proper handling and releasing of angled fish; mortality may be higher in areas with less experienced anglers. Other fac-

TABLE 4.—Fate of angler-caught-and-released, radio-tagged steelhead in the Vedder–Chilliwack River, British Columbia, by the number of subsequent recaptures reported. Data for the study years 1999 and 2000 are combined.

Fate	Number of reported recaptures: Zero	One	Two	Three
Died or regurgitated tag	10	0	0	0
Killed by angler	8[a]	25	4	1
Spawned and died	31	8	1	1
Spawned and kelted	104	20	4	1
Unknown; tag removed[b]	0	2	3	1
Unknown	1	1	0	0
Total	154	56	12	4

[a] Unreported recaptures inferred from the abrupt disappearance from popular fishing locations of fish with multiple detections.

[b] Radio tag removed by angler upon recapture, and fish released alive.

TABLE 5.—Recapture frequency and fate of caught-and-released, radio-tagged steelhead in the Vedder–Chilliwack River, British Columbia, by run-timing component. Early-run fish were tagged in December or January, middle-run fish in February or March, and late-run fish in April or May. Data were pooled for the 1999 and 2000 study years. Information is not available for 10 fish that either died or regurgitated their tags following tagging.

	Recaptures		Fate[a]	
Run	Recaptured	Not recaptured	Harvested	Spawned
1999				
Early	5	7	1	10
Middle	16	20	4	32
Late	4	19	2	19
2000				
Early	33	26	19	36
Middle	16	32	8	39
Late	6	32	4	34

[a] The fates of six fish whose radio tags were removed by anglers upon recapture could not be determined. The fates of two other fish are unknown.

tors might artificially reduce mortality rates in this study. The presence of observers (the fishery technicians who tagged the fish at the initial capture) might cause anglers to modify their normal methods of handling fish (e.g., reducing air exposure). However, mortality rates were also low for angler-reported recaptured fish, where there was no observer effect. Anglers may have chosen to retain badly injured hatchery fish, thus reducing the apparent mortality from catch and release. However, mortality rates were also low for wild fish, which must be released.

The minimum survival of unharvested fish from initial capture to spawning was greater than 92% for both wild and hatchery steelhead in both years; the removal of radio tags from some recaptured fish meant that we could not track the fate of these fish, and actual survival may be slightly higher, as suggested by our mortality estimate. There was no evidence for delayed mortality; fish that died usually did so within a few days of release. Thus, the hooking mortality rates determined from the many shorter-term studies in the literature probably provide accurate measures of the effects of catch-and-release angling. There was no evidence that the physiological stresses associated with multiple recaptures of a fish by anglers reduced postspawning survival to kelting. The survival estimates also imply that prespawning natural mortality was less than about 4% in the Chilliwack River.

The in-river behavior of hatchery and wild steelhead differed despite the hatchery fish's being the F_1 progeny of native, wild parents collected throughout the watershed. The spatial distributions of hatchery and wild fish during the prespawning period were similar, and thus, their interactions with the fishery might be expected to be similar. However, hatchery fish were reported recaptured at twice the rate of wild fish. Reporting bias (i.e., the under-reporting of recaptures of wild fish) seems unlikely to account for this difference. We do not expect differential reporting for fish that were caught and released because the effort to report the recapture is the same for both wild and hatchery fish, and there is no obvious disincentive to reporting a wild fish. However, an angler who illegally harvested a wild fish might not report the fact. Nonreporting of some recaptures certainly occurred; we noted the abrupt disappearance of seven unreported tags, which we assumed to represent angler kills. However, six of these unreported recaptures were hatchery fish, which data do not indicate a higher underreporting rate for harvested wild fish. Moreover, because we can account for the fate of all but one of the radio-tagged wild fish (Table 1), there is little scope for the reported recapture rate to be influenced by the unreported harvest of wild fish.

Other studies have also found that hatchery-origin salmonids have a higher susceptibility to angling than wild fish (Dwyer 1990; Mezzera and Largiader 2001), but the hatchery fish in these studies were nonnative or domesticated stocks whose behavior might be expected to differ from that of the native stock. In contrast, we expected hatchery-reared steelhead in our study to be similar to wild fish because the broodstock was drawn annually from the wild, native population. The presumed genetic similarity of hatchery and wild fish in our study and the fact that both wild and hatchery fish would experience similar environmental conditions from smolting onward suggest that the response of adult steelhead to angling was influenced by their different early rearing environments. Nevertheless, inadvertent selection during broodstock collection or rearing was possible. It is tempting to speculate that the collection of hatchery broodstock by angling might select for aggressive behavior in adults. Higher levels of aggression have been noted in hatchery-reared salmonids (summarized in Weber and Fausch 2003), but the basis of the behavior is uncertain.

Hatchery programs with a goal of providing harvestable fish while minimizing adverse effects on native steelhead often attempt to segregate wild and hatchery fish in time or space (Ludwig 1995; McLean et al. 2004). The overlap in the spatial distributions of hatchery and wild adults seen here during the prespawning holding period will reduce the ability of fishery managers to direct angling mortality away from wild fish, despite their lower catchability. However, the observed difference in spawning distributions between wild and hatchery steelhead—half the wild fish spawning upstream of the hatchery fish—will maintain partial reproductive isolation between the two stock components, despite temporal overlap in spawning. Without direct observations of mating or genetic markers to assess parentage, we cannot determine the extent to which the overlap in spawning distributions in the lower river led to introgression between hatchery-origin and wild-origin fish. The spawning distribution of hatchery fish, near the hatchery site at which they were incubated and reared to smolt stage, rather than near the downstream smolt release site, was consistent with other studies that found that the proportion of adults returning to their rearing site increased as the separation between rearing and release sites decreased (Slaney et al. 1993; Dittman and Quinn 1996). Dittman and Quinn (1996, p. 87) suggested that ‘‘salmon may initially return to their site of release, but if they can detect the odors of their rearing site they will continue on to this site.’’ The location of the hatchery in the middle portion of the watershed and the close proximity of smolt release sites to the hatchery will limit the ability of managers to restrict the spatial distribution of hatchery spawners to areas little-used by wild fish and, thus, to limit interbreeding.

Early-run fish were exposed to the sport fishery for much longer periods than late-run fish and in 2000 at least were recaptured and killed by the fishery in much higher proportions than late-run fish. Run timing is heritable in salmonids (Stewart et al. 2002), and may be correlated with spawning location (Webb 1998). Thus, the sport fishery may be selecting against specific subcomponents of the population.

Both segregation and supplementation are possible management options for using hatchery programs to maintain fisheries on low-abundance populations of steelhead. Our data have important implications for both types of hatchery programs. Our spatial distribution data suggest that (1) habitat conditions (e.g., the spatial distribution of potential holding sites) may result in a common fishery, even where management intent is to segregate hatchery and wild fish, (2) phenotypic effects of rearing environments may be important modifiers of spawning distributions, even when hatchery fish (presumably) share a high degree of genetic similarity with wild fish, and (3) supplementation programs, which are intended to augment the natural breeding population by allowing interbreeding between closely related hatchery and wild fish, may not necessarily result in substantial interbreeding. Our survival data indicate that catch-and-release angling imposes relatively small costs in terms of survival to spawning and kelting in this population of winter steelhead and that the sport fishery may select against specific timing groups (early run) within the population. The effective integration of hatchery programs and harvest management to achieve societal objectives for low-abundance populations of steelhead will require the explicit consideration of effects such as those noted in this study.

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