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[Article]

Comparison of Adult Steelhead Migrations in the Mid-Columbia Hydrosystem and in Large Naturally Flowing British Columbia Rivers

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Abstract.—The migration of 1,263 adult radio-tagged steelhead *Oncorhynchus mykiss* was assessed in the Nass, Skeena, Bella Coola, Fraser, and mid-Columbia rivers from 1993 to 2001. Of the summer-run steelhead tagged in the mid-Columbia River, 80–87% eventually continued their upstream migration after being tagged, and 87–90% of those were detected in spawning areas. Similar results were seen for summer-run steelhead tracked on the Nass and Skeena rivers. Mid-Columbia summer-run steelhead stocks that passed five dams en route to their spawning destinations (Methow and Okanogan rivers) traveled at a median rate of 20 km/d, which exceeded the median rates for summer-run steelhead tracked on the Nass (3.8 km/d) and Skeena rivers (12–16 km/d). The upstream migration rates were best explained by river gradient and distance of the study area from the ocean. When the effects of river gradient and reach location were taken into account, impoundment was still a significant factor increasing the upstream migration speeds of summer-run steelhead. Kelting speeds varied widely among rivers and did not appear to be a function of gradient.

Radiotelemetry techniques have been used to study the migration of adult salmonids on the Columbia River system since 1957 (Johnson 1960), yet the information available for steelhead *Oncorhynchus mykiss* in the mid-Columbia River (i.e., the Columbia River between the confluences of the Snake and Okanogan rivers; Figure 1) is sparse. Although 850–3,000 upstream-migrant steelhead were radio-tagged and released each year in the lower Columbia River from 1996 to 1998 (Keefer et al. 2004), less than 3% migrated up the main stem far enough to reach the mid-Columbia area (Alexander et al. 1998; English et al. 1998). The first major radiotelemetry study of adult steelhead migration through the mid-Columbia River was conducted in 1999–2000, when 395 fish were tagged and released directly into the study area (English et al. 2001). The study was repeated in 2001–2002 (English et al. 2003). These two studies provide the majority of what is known about steelhead migrations and spawning success in the mid-Columbia River.

Since the early 1990s, there have been several large-scale radiotelemetry studies of steelhead migration rates and spawning success conducted on British Columbia (BC) rivers. In 1993, summer-run steelhead were studied on the Nass River (Alexander and Koski 1995). On the Skeena River, summer-run steelhead were studied in 1994 and 1995 (Koski et al. 1995; Alexander et al. 1996). Fall and winter-run steelhead were studied on the Fraser River from 1996 into 1997 (Nelson et al. 1998; Renn et al. 2001). Also in 1997, a study of Bella Coola River spring and fall-run steelhead was conducted (English et al. 1999). One of the goals of this paper is to combine data from all these studies to evaluate the effects of river, run type, stock, and year on steelhead migration rates, travel times and tracking success. Knowledge of stock-specific migra-

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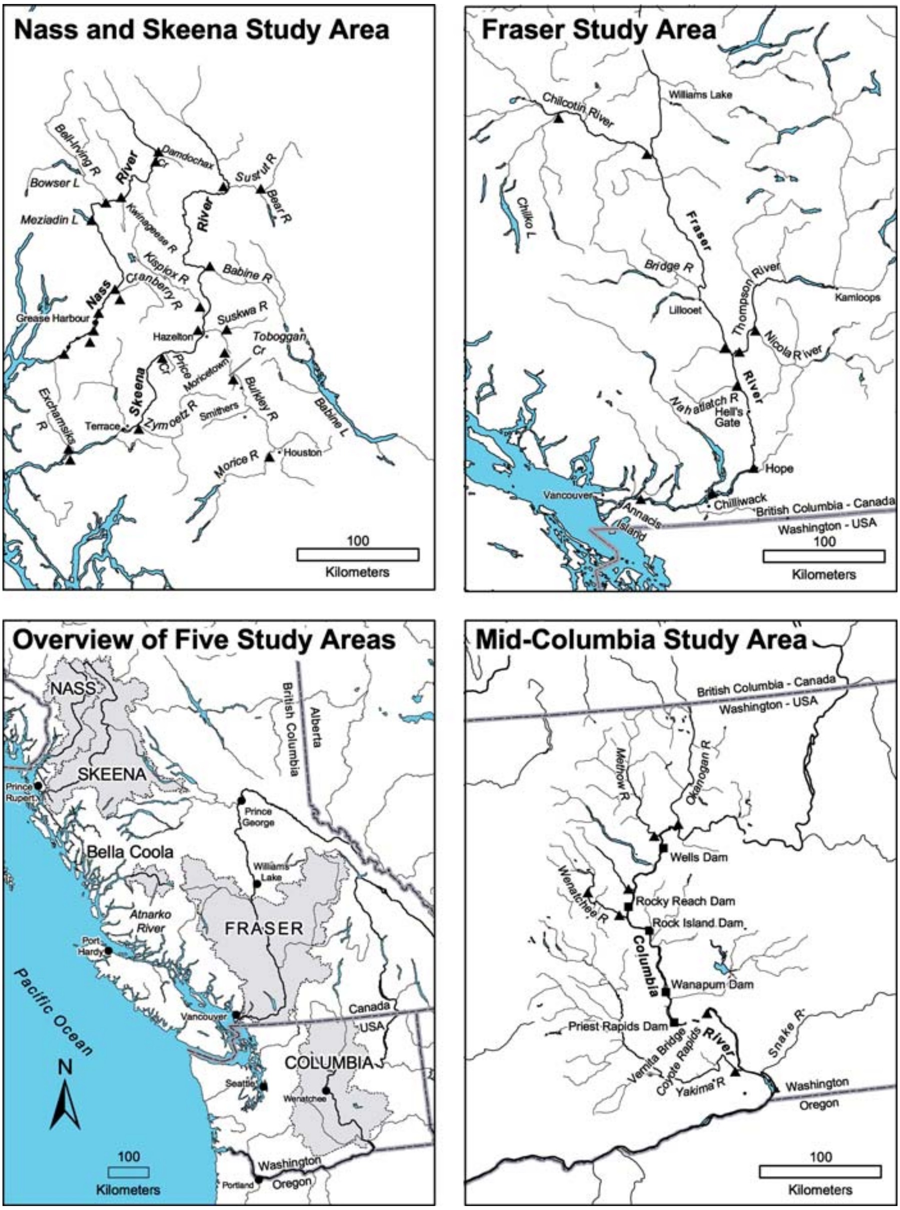

FIGURE 1.—Map showing the watersheds of the five study areas (shaded areas in the lower left panel) and the locations of the fixed-station receivers (triangles) used in the Nass and Skeena (upper left panel), Fraser (upper right panel), and mid-Columbia River (lower right panel) studies. Monitoring arrays at the five mid-Columbia dams are marked with squares.

tion rates is important to make informed decisions about in-river fisheries, especially in rivers shared by both targeted and protected stocks.

Another goal of this paper was to compare migration and kelting rates between mid-Columbia River steelhead (which must navigate past as many as five dams between their release site and their spawning ground) and steelhead in naturally flowing BC rivers. Using radiotelemetry-derived estimates of migration and kelting rates (i.e., the directed downstream movements of steelhead after spawning), we explored whether the challenges presented in an impounded river system are more severe than those in more naturally flowing rivers. Decisions to build or breach dams should be made with an understanding of the effects of impoundment on the ecology of steelhead populations.

Our knowledge of such effects is limited by the paucity of data from rivers where steelhead populations were studied both before and after impoundment. As such, we can best study the effects of impoundment by making comparisons among rivers. In this paper, we limited most comparisons to summer-run steelhead in order to reduce variation in temperature among rivers. Variation in river length and gradient were treated statistically.

Methods

The seven steelhead radiotelemetry studies described in this paper employed a variety of fish capture and tracking techniques but used similar radio tags and tracking technology. Maps of each study area showing the release and fixed-station receiver (monitoring) sites are provided in Figure 1. All location names mentioned in this paper can be found in Figure 1.

All of the tags and receivers used in these studies were manufactured by Lotek Engineering, Inc. Several different types of Lotek tags were used depending on the size of the fish and goals of the study. Most tags (98%) measured 14.5–16.2 mm in diameter, 43–51 mm in length, and weighed 10.7–16.0 g in air (4.2–12.8 g in water). However, in the 1993 Nass study, 19 of the tags applied were exceptionally large (16.2 mm diameter, 83 mm length, 29 g in air, 12.8 g in water) and were applied only to steelhead longer than 72 cm. The manufacturer's minimum battery-life guarantee for the tags ranged from 8.6 to 25 months. In all studies, each radio tag emitted a unique signal, thereby allowing real-time recognition of individual fish. Due to programming limitations, a limited number of unique codes existed for any given broadcast frequency. As such, several different broadcast frequencies ("channels") were used, drastically increasing the number of tags that could be uniquely identified. Depending on the study, from 3 to 13 channels were used. In all studies, receivers were programmed to repeatedly scan through each of the channels, spending slightly more time on each channel than the interval between tag transmissions (which also varied among studies), before continuing on to the next channel.

The tagging and sampling procedures varied little among studies. The fish were held while immersed in water, and an external (anchor or spaghetti) tag was applied, nose-to-fork length was measured, the sex was identified, an examination for external marks was performed, a few scales were removed for aging analysis, and a radio tag was gastrically inserted (i.e., inserted through the mouth into the stomach, see Winter 1983) with the antenna protruding from the corner of the mouth. In some cases, a DNA sample was taken from the adipose fin. The tagging procedure generally took less than 1 min.

With the exception of the 1993 Nass River study, the primary focus of these studies was to monitor steelhead movements. The Nass steelhead study was conducted opportunistically with a larger radiotelemetry study of Chinook salmon *O. tshawytscha* behavior (Koski et al. 1996a). Reports from each study described the swim speed, final locations and stock composition of the tagged fish, along with ancillary information such as the proportion that drift downriver, die, or vanish after tagging. In the following sections, we describe study-specific methodologies, including fish capture and handling techniques. Subsequent sections describe the methodologies that were common across all studies, including the fixed-station setups, the mobile tracking techniques, and the data processing procedures.

Mid-Columbia River, 1999 and 2001.—Fish capture and tagging operations were carried out at the exit trap in the east bank fishway of Priest Rapids Dam (English et al. 2001, 2003), located 639 km from the mouth of the Columbia River. Twice a week from 15 July to 14 October, all fish were directed through the trap for sorting and sampling. Healthy adult steelhead were netted from the trap and placed in an anesthetic bath (tricaine methanesulfonate [MS-222]) for biological sampling. The tagged steelhead were transferred to a transport truck, and released about 12.7 km downstream of Priest Rapids Dam, at Vernita Bridge. To ensure appropriate conditions for tagging, transport and release, water temperature and dissolved oxygen concentration were monitored regularly in the fishway, sampling bath, tagging bin, transport truck, and at Vernita Bridge. Each year 395 radio-tagged steelhead were released.

Nass River, 1993.—Steelhead capture and tagging was conducted in the lower Nass River, 30–50 km from the river mouth, from 13 July to 8 October 1993 (Alexander and Koski 1995), but the bulk of the fish (85%) were tagged in July and August. Most of the steelhead were caught using fish wheels, which are described in detail by Link and English (1996). Both early and late in the season, tangle nets were used to supplement the fish wheel catches. The tangle nets (15 cm mesh, 3 m deep, and 45 m long) were fished at several sites ranging from 1 km below to 5 km above the fish wheels. Fish were not anesthetized as the effects on fish edibility were unknown at the time. In all, 66 radio-tagged steelhead were released.

Skeena River, 1994.—Commercial seine boats were the primary tool used to capture steelhead and coho salmon *O. kisutch* in marine waters near the mouth of the Skeena River from 13 July to 29 August 1994 (Koski et al. 1995). Seine fishing effort ranged from three to nine vessel-days per week. Using commercial braille fisheries methods, the seine was set, pursed and brought alongside the boat. Steelhead and coho salmon were removed from the seine, two to four at a time, and placed in holding tanks onboard the seiner. All healthy steelhead and coho salmon were moved to a tagging trough and measured. Only those longer than 50 cm were radio-tagged. During the processing of these fish, the remaining coho salmon and steelhead were left in the seine alongside the boat. From 21 August to 11 September 1994, additional steelhead were captured and tagged using fish wheels at Kitselas Canyon (137 km upstream from the mouth of the Skeena River). Fish were tagged on the fish wheel platform and released directly into the river immediately after tagging.

Skeena River, 1995.—From 23 July to 19 September 1995, fish wheels at Kitselas Canyon were used to capture 100 steelhead for radio-tagging on the lower Skeena River. Fish handling and tagging procedures were similar to those described above for the Skeena fish wheels in 1994. However, a portion of the fish were transported after tagging and released into a calm water area.

Fraser River, 1996–1997.—Angling and tangle netting were used to catch steelhead in the fall of 1996, and angling was used during the winter–spring of 1997. The fall 1996 angling effort occurred near Chilliwack (90 km from the river mouth) where tags were applied from 25 September to 4 November. The winter–spring angling occurred upstream from Hope (river km 154) from 5 February to 8 May 1997. Tangle netting was conducted in the vicinity of Annacis Island (near the upstream end of the Fraser delta, 21 km from the river mouth) between 23 September and 10 November. The tangle net was constructed of 8.9 cm mesh that would entangle fish by the kype and fins but not by the gills. Captured steelhead that were suitable for tagging were anesthetized in a clove oil and ethanol solution. In all, 161 radio tags were gastrically inserted. The fish were then returned to the holding tube for recovery before release (Nelson et al. 1998; Renn et al. 2001). Fraser River fish were excluded from comparisons of upstream migration rates, since these comparisons were restricted to summer-run stocks.

Bella Coola River, 1997.—Thirty-two adult steelhead were captured by angling and tagged during two distinct intervals in 1997. Spring-run steelhead were tagged in the lower reaches of the Bella Coola watershed (5–35 km from the river mouth) from 24 March to 22 May. Fall-run steelhead were tagged in the middle and lower reaches of the Atnarko River (75–80 km from the mouth of the Bella Coola River) from 27 October to 7 December. No anesthetic was used. Bella Coola fish were excluded from comparisons of upstream migration rates, since these comparisons were restricted to summer-run stocks.

Tracking methods.—Fish migration rates and spawning destinations were determined by combining data obtained from fixed-station receivers with those from mobile tracking efforts. The radiotag receiver used for both fixed-station and mobile tracking was the SRX 400 built by Lotek Engineering, Inc., with their Code Log data processing and storage program.

Complete detection histories were resolved for each radio-tagged steelhead. Detection histories were summarized in a matrix of ones and zeros that denoted the presence or absence of each fish at each fixed-station site (and at upriver spawning locations). Knowledge of which sites had to be passed in order to arrive at more upstream locations allowed for the detection efficiency (the ratio of the number of radio-tagged steelhead detected to the number of radio-tagged steelhead known to have passed) to be determined for each of the fixed-station sites.

Fixed stations.—In each study, fixed-station tracking systems were established at strategic locations to maximize detection rates of fish moving along the main stem or entering known spawning tributaries. In the Nass River study, the location of Chinook salmon spawning areas was the key factor in selecting the fixed-station sites and allocating mobile tracking effort. In the 1994 Skeena River study, fixed-station sites were selected to achieve the study objectives for both steelhead and coho salmon.

Each fixed station consisted of one, two, or three Yagi antennas and a receiver, which was powered by a 12-V deep-discharge battery. Where available (e.g., at the dams), AC power was used to constantly charge the 12 V battery. At several of the remote stations, a solar panel was used to charge the battery. In general, sites near high tension power lines or other sources of environmental noise were avoided and detection efficiencies were good at all the critical fixed-station sites.

Koski et al. (1996b) described the operation of the antenna switching units that were used for detecting fish and for determining the direction of fish movements. Basically, an antenna was set up to monitor the river upstream of the receiver site, and another antenna was set up to monitor downstream. Stations located at a tributary confluence had a third antenna positioned to detect fish entering and exiting the tributary. The strength of the signal detected by each antenna can be used to determine a fish's position relative to the receiver. In order to maximize detection probability, all antennas were monitored simultaneously until a signal was detected, at which time the receiver would scroll through each antenna individually to determine the location and strength of the signal.

At each of the five mid-Columbia River dams, an array of fixed stations was deployed, employing both aerial and underwater antennas. Aerial antennas monitored the tailrace area approaching the dam, and the forebay areas upstream of the fishway exits. Underwater antennas were used in the fishways and in the spillway to monitor upstream progress and fallback. Each array was designed to record the arrival and departure of radio-tagged fish and to monitor movements of these fish into the fishway entrances, collection channels and through the fishway exits. As such, the monitoring effort at the dams was considerably greater than that at standard fixed-station monitoring sites. The effect of this increased monitoring effort was that detection efficiencies were improved. Improved detection efficiencies meant higher sample sizes for assessments of migration behavior, but had no effect on the point estimates of migration rates, or on any of the metrics of interest in this study.

Mobile tracking.—Mobile tracking, which was used to estimate spawning location, was conducted by means of helicopters, planes, and boats as well as on foot.

Aerial tracking was conducted by means of helicopters or fixed-wing aircraft with one or two three- or four-element Yagi antennas attached to the aircraft's cargo skids, struts, or nose. The aircraft was flown along the river and its tributaries at 80–130 km/h and at 90–300 m above ground level. The location and identities of each fish were determined by means of a GPS with a built-in data logger and by the SRX 400 receiver, respectively. During most surveys, two receivers were operated on different channels so that the probability of passing a fish without recording it was reduced. Most aerial telemetry data were obtained during trips to download and service the fixed-station receivers.

Tracking was also conducted from a boat and on foot on an opportunistic basis. Most foot survey data were collected when conducting counts of live steelhead to determine mark rates in various tributaries. However, some data were collected while visiting fixed-station receivers to download data, while tagging fish at the various in-river sites, or while monitoring local fisheries. Foot and boat tracking procedures were similar to those used on the aerial surveys.

Data processing.—An important component of radiotelemetry studies is the removal of false records in receiver files (e.g., those that originated from electronic noise). In these studies, records were considered invalid if they had power levels less than 50 (on a 1–232 scale), if less than two detections occurred within the same zone within 20 min, and if earlier and later records for the same radio-tagged individual were recorded on zones that were too distant to be realistic.

The raw data were filtered to remove false records and queried to produce a compressed database containing the sequential detections for each radio-tagged fish. The compressed database was used to determine when each fish arrived at and departed from each fixed station, residence times at each station or spawning area, rates of movement between detection sites, and sites of last detection.

Tracking analyses.—Three sets of metrics were defined for the comparison of results from each of the studies. One set was used to assess the effects of the capture, handling and tagging operations by examining fish behavior patterns immediately after tagging. The second set was used to assess the tracking-migration success for fish that resumed their migration after being tagged. The third set was used to describe the kelting behavior and included data from all radio-tagged steelhead that were tracked to tributary spawning locations above the release sites.

The effect of the tagging procedure was assessed by identifying the fish that did not resume their upstream migration after release. The proportion of the release that was available for detection and recovery upstream of the release site (ϕ_1) was determined as

$$\phi_1 = (M - S_b - L)/M,$$

where M is the total number of radio-tagged steelhead released; S_b is the number of radio-tagged fish tracked to spawning sites below the release site; and L is the known losses of tagged fish. Losses included the number of tags that were stationary near the release site (i.e., regurgitations or mortalities), the tags that were never tracked (i.e., tag malfunction or fish that migrated downstream undetected), the radio-tagged fish that were caught in fisheries below the first detection zone (based on tag returns); and the radio-tagged fish that were tracked to nonspawning areas below the release site. In several studies, the release sites were upstream from some known steelhead fisheries and spawning areas.

For those fish that resumed their upstream migration after tagging, our measure of tracking-migration success was

$$\phi_2 = (S_a)/(M - S_b - L - R_a),$$

where S_a is the number of radio-tagged fish tracked to a spawning destination above the release site and R_a is the number of radio-tagged fish removed in fisheries conducted above the first upstream detection site. The ϕ_2 metric is a function of tracking effort (fixed-station and mobile), tag recovery, our knowledge of steelhead spawning locations and the individual fish's ability to reach a known spawning area.

Information on the behavior of the radio-tagged steelhead after spawning was obtained primarily from the fixed-station receivers located downstream from known spawning areas. The portion of each steelhead stock that migrated downstream as kelts (ϕ_3) was

$$\phi_3 = K_t/S_t,$$

where S_t is the number of radio-tagged steelhead tracked to the tributary spawning areas and K_t is the number of these steelhead that were tracked moving downstream from their tributary spawning area after the spawning period. The downstream migration speed for kelts was also estimated for fish detected at more than one fixed station during the kelting period.

Comparisons of the three metrics among studies were performed using the Kruskal–Wallis test, which was appropriate since the dependent variables were not normally distributed. It is important to note that the sample sizes were very small for the among-study comparisons (there was only one data point per study). As such, it is very unlikely to find statistical significance at the 0.05 level. When statistical significance is achieved, it is likely a robust result. The same cannot be said of tests showing no difference. The *P*-values have been reported for completeness, but should be interpreted with caution: significant *P*-values should be interpreted as strong results, whereas nothing can be said for certain about nonsignificant *P*-values.

Stock assessments.—Fish tracked to a known spawning area were assumed to be part of that local stock.

In the 1999–2000 mid-Columbia River study, 85 radio-tagged fish were assigned to the Wenatchee stock, 90 to the Methow stock, and 50 to the Okanogan stock. The large majority of Methow (89%) and Okanogan (93%) fish were hatchery reared. Hatchery fish made up a smaller proportion of the Wenatchee stock (64%). In the 2001–2002 study year, the Wenatchee, Methow and Okanogan stocks were represented by 47, 144 and 69 radio-tagged individuals, respectively. Again, hatchery fish made up the large majority of Methow (80%) and Okanogan (90%) fish, and a smaller proportion of the Wenatchee stock (52%). In both studies, other stocks were poorly represented in the sample, and were ignored in all analyses of upstream migration except where noted.

For the purposes of this study, among-river comparisons were restricted to summer-run stocks (see below). Three BC studies included summer-run stocks: the 1994 Skeena study, the 1995 Skeena study and the 1993 Nass study. Except where otherwise noted, only ocean-tagged steelhead were included in analyses involving the 1994 Skeena River study. Ten radio-tagged steelhead were assigned to the Kispiox stock, 12 to the Babine stock, 5 to the Sustut stock, 21 to the Bulkley Stock, and 5 to the Morice stock. In the 1995 Skeena River study, the Kispiox, Babine, Sustut, and Bulkley stocks were represented by 5, 12, 3, and 14 radio-tagged individuals, respectively. There was only one radio-tagged Morice fish. In the 1993 Nass River study, individual stocks were poorly represented in the sample, hence stocks were pooled into "lower Nass," "middle Nass," and "upper Nass" groupings. Overall, 6, 11, and 13 radio-tagged fish were assigned to these three groupings. In general, too few fish were assigned to stock groupings for the 1993 Nass study and the 1995 Skeena study to make strong statistical among-stock comparisons. For all three studies, radio-tagged fish that were not assigned to one of the above mentioned stock groupings were ignored in all migration analyses except where noted.

Analyses of migration behavior.—Comparisons of stock-specific migration rates were restricted to those through the lowermost reaches within each study area, since most of the stocks must migrate through the lower parts of the river en route to their respective spawning areas. Moreover, comparisons of upstream migration behavior were restricted to summer-run stocks. Of greatest interest was the contrast between the mid-Columbia and BC rivers. Since the mid-Columbia steelhead are summer-run, it was necessary to exclude BC stocks running during fall, winter and spring in order to minimize the influence of temperature and run type on the among-river differences in migration behavior.

Migrations rates were calculated for each individual, j, within each reach of each river as

$$v_{jsr} = d_{sr}/t_{jsr},$$

where d_{sr} was the distance between the fixed stations on either end of reach s within river r and t_{jsr} was the time required for individual j to travel from one end of reach s to the other. Travel times were calculated as the time between the first detection at the downstream fixed-station receiver and the first detection at the upstream fixed station. For within-individual comparisons (e.g., migration rate in one river reach versus the next), parametric-matched pair statistics were used, as the distribution of differences between the paired observations tended to be normally distributed.

Grouping the individuals into stocks allowed median stock-specific migration rates to be calculated for each reach within each river. Median stock and reach-specific migration rates were compared using the Kruskal–Wallis test.

For each river, median river-specific migration rates were calculated by grouping the v_{jsr} values by river. River-specific migration rate calculations included data from individuals assigned to a stock (or stock grouping), and included data from all reaches except those adjacent to the release site and those adjacent to the individual's spawning tributary.

Since the delays that occurred at each of the dams were not included in the within-reach migration rates, the real rate of travel through the mid-Columbia must be slower than that calculated using the above method. As such, a second set of among-river comparisons was performed, based on large, representative river reaches. One representative reach was selected for each study. Selection of the reach that would represent each study involved balancing the trade-off between encompassing as much of the main-stem river as possible (by selecting a larger reach) and maximizing sample size (by selecting a smaller reach). The selected reaches for each study were located close to the release site in order to include data from as many lower-river stocks as possible (as these leave the main stem relatively close to their release site, and reaches that encompass too much of the upper river will include data from fewer stocks). The mid-Columbia River reach extended from the tailrace of Priest Rapids Dam to the forebay of Wells Dam (192 km, 114 m vertical gain), thus the lower-river stocks and the Wenatchee stock were not included in this analysis. The 1994 Skeena River reach extended from the Exchamsiks junction to the Bulkley junction (203 km, 216 m vertical gain). An alternative and much smaller 1994 Skeena reach was the same as the one used in 1995. During the 1995 Skeena study, the radio-tagged fish were released mid-river, thus the lower parts of the river could not be included in the reach. As such, the 1995 Skeena River reach extended from the Price Creek junction to the Bulkley junction (46 km, 46 m vertical gain). The Nass River reach extended from Grease Harbour to the Cranberry junction (30 km, 64 m vertical gain). The distances between the fixed stations were derived from digital maps. Travel times were calculated as the time between the first downstream detection and the first upstream detection. This analysis included radio-tagged fish that were not assigned to a stock grouping, and included 1994 Skeena fish regardless of release site.

The upstream migration rates, calculated for one large reach within each study area, were compared among rivers by means of the Kruskal–Wallis test. Trends associated with river gradient and tagging location (kilometers upstream from river mouth) were explored using linear regression. Later, the effects of impoundment, gradient and tagging location were estimated using multiple regression. This allowed the effects of impoundment to be assessed after accounting for gradient and tagging location.

To compare kelting speed (the speed of the directed downstream movements of steelhead after spawning) among rivers, a single representative reach was selected from each river and a median downstream migration rate was calculated. The river reaches were selected to maximize distance as well as sample size. The mid-Columbia River reach extended from the Rock Island Dam to Coyote Rapids in the Hanford area (114 km, 51–65-m vertical drop). The Skeena River reach extended from the Bulkley junction to the Exchamsiks junction (203 km, 216-m vertical drop). The Fraser River reach extended from the Thompson River junction to Hope (101 km, 61-m vertical drop). Only fish that were assigned to tributary spawning sites were included in the analysis. Fraser steelhead were not summer-run. For the Skeena River studies, only ocean and fishwheel releases were included. Statistical comparisons were made using the Kruskal–Wallis test. Trends associated with river gradient and tagging location were explored using linear regression.

Results

Tracking Analyses

Tagging success (ϕ_1) for studies where tags were applied in the fall, winter, or spring ranged from 88% to 100%. The proportion of tagged summer-run steelhead that were tracked upstream of the release site was significantly lower, ranging from 45 to 87% (Table 1; $\chi^2 = 7.5$; $P = 0.006$). Of the summer-run steelhead, the mid-Columbia River stocks had the highest proportion of tagged fish that resumed their upstream migration after release and remained upstream through the spawning period (80–87%; compared with 45–73% for BC rivers; $\chi^2 = 3.4$; df = 1; $P = 0.06$). An additional 5% of the fish tagged on the mid-Columbia migrated upstream shortly after release but later migrated downstream to spawning areas below the release site.

After accounting for the various types of losses, including known fishery removals, the proportion of radio-tagged fish that were tracked to upstream spawning areas (i.e., the tracking and migration success, ϕ_2) was consistently high for summer-run steelhead (83–100%). The tracking and migration success for mid-Columbia steelhead (87–90%) was similar to that observed for summer-run steelhead on the Nass (86%) and Skeena rivers (83–100%; Table 1; $\chi^2 = 0$; df = 1; $P = 1$). The tracking and migration success of fall, winter and spring-run stocks (42–100%) was not significantly different from that of summer-run stocks (Table 1; $\chi^2 = 0.54$; df = 1; $P = 0.46$).

Of the mid-Columbia River steelhead that were

TABLE 1.—Summary of tagging, tracking and migration success, and kelting rates for radio-tagged steelhead released on the mid-Columbia River and four rivers in British Columbia. Where appropriate, model variable symbols are given in parentheses.

Variable	Bella Coola	Fraser	Bella Coola	Fraser	Fraser	Skeena	Skeena	Skeena	Nass	Mid-Columbia	Mid-Columbia
Year	1997	1997	1997	1996	1996	1994	1995	1994	1993	1999	2001
Capture method	Angling	Angling	Angling	Angling	Tangle net	Seine	Fish wheel	Fish wheel	Fish wheel	Trap	Trap
Run	Spring	Winter	Fall	Fall	Fall	Summer	Summer	Summer	Summer	Summer	Summer
Travel distances (km)											
Ocean to release site	20	143	77.5	95	22	0	142	142	60	625	625
Release site to spawning areas	10–120	50–200	10–40	100–500	100–500	100–400	20–300	20–300	100–400	130–250	130–251
Number of tags											
Tags applied (M)	24	82	8	50	29	113	100	42	66	395	396
Downstream spawning areas (S_b)	0	0	0	0	0	0	0	2	0	46	22
Tag losses (L)											
Stationary near tag site	0	2	1	0	0	0	0	2	3	10	9
Fish never tracked	0	4	0	0	2	30	0	1	9	2	2
Other downstream areas	0	0	0	0	0	0	37	18	9	22	18
Known fishery recoveries (R_a)	0	3	0	2	3	9	3	2	2	13	23
Upstream spawning areas (S_a)	24	65	7	21	10	68	50	17	37	262	291
Upstream tributary spawning areas (S_t)	24	65	7	21	10	66	50	17	28	230	268
Kelted (K_t)	17	46	4	9	5	36	27	8	n/a	n/a	170
Proportions (%)											
Tagging success (ϕ_1)	100	93	88	100	93	73	63	45	68	80	87
Tracking and migration success (ϕ_2)	100	89	100	44	42	92	83	100	86	87	90
Tracked moving downstream (ϕ_3)	71	71	57	43	50	55	54	47			63

tracked to tributary spawning areas in 2001, 63% were detected migrating downstream after the spawning period in 2002. This rate (ϕ_3) was higher than any summer-run or fall-run steelhead on the Nass, Skeena, Fraser and Bella Coola rivers, but the difference was not statistically significant (Table 1; $\chi^2 = 2.2$; df = 1; $P = 0.13$). Spring-run and winter-run steelhead had significantly higher kelting rates (71%; $\chi^2 = 4.2$; df = 1; $P = 0.04$) than summer or fall runs.

Upstream Migration Behavior

Mid-Columbia River.—For mid-Columbia River stocks, the distribution of travel times was consistent between the two study years (Table 2). Within a year, travel times and migration rates were remarkably similar among stocks (Figure 2; Table 2). Of the 10 among-stock comparisons (5 reaches by 2 years), only one was statistically significant (Table 2; between Rocky Reach and Wells dams, 2001; $P = 0.013$). This result was not statistically significant when the alpha was adjusted for the number of comparisons made (Bonferroni adjustment). Moreover, the 10% difference in migration rates between stocks (39.9 versus 43.9 km/d) was not likely to be biologically significant.

An observation that was consistent among stocks and between years was that individuals had relatively slow migration rates in the river reach immediately upstream of the release site (Table 2). This statistically significant effect (matched pairs *t*-tests; one tailed *t*-values from 9.7 to 23.4; $P < 0.0001$) was probably a result of post-tagging recovery and similar processes.

Delays in migration that resulted from dam passage were less than 1 d for all stocks at all five dams in both years (Table 3). In both years, the fastest dam passage occurred at Rock Island, where median dam passage was 8.4 h or less for all stocks/years (Table 3). In 1999, there were no statistically significant differences among stocks in passage time at any dam (Table 3; $P > 0.05$). The same was true in 2001, except for the difference between the Priest Rapids passage times for Wenatchee and Methow fish and that for Okanogan fish (Table 3; $\chi^2 = 7.6$; df = 2; $P = 0.023$). As mentioned above, this result was not statistically significant when the alpha was adjusted for the number of comparisons made (Bonferroni adjustment).

A robust result, consistent among stocks and between years, was that individuals slowed down significantly in the main stem adjacent to their spawning tributary (Figure 2; Table 2). For example, in 1999 Wenatchee fish moved between Wanapum and Rock Island at a rate of 31.3 km/d, then slowed significantly to 4.0 km/d between Rock Island and the Wenatchee confluence (Table 2; $t = -17.8$; df = 59; $P < 0.0001$). Similarly, 2001 Methow fish, which traveled at 39.9 km/d between Rocky Reach and Wells, slowed significantly to 3.7 km/d between Wells

TABLE 2.—Median migration rates (km/d) by Columbia River steelhead stock and river reach in 1999 and 2001 (95% confidence bounds in parentheses). Chi-square tests test for within-reach differences among stocks. One-tailed, matched-pair *t*-tests test for differences between the "last" river reaches (those adjacent to the tributary spawning destination) and the "penultimate" river reach as well as between the first and second river reaches. Abbreviations are as follows: PR = Priest Rapids Dam; WA = Wanapum Dam; RI = Rock Island Dam; RR = Rocky Reach Dam; and WE = Wells Dam; NS = not significant.

Reach and *t*-test	Wenatchee stock	Methow stock	Okanogan stock	χ^2
1999				
Main-stem reaches adjacent to spawning tributaries				
RI to Wenatchee River	4.0 (2.1–7.3)			
WE to Methow River		6.6 (3.0–12.2)		
WE to Okanogan River			19.6 (7.6–30.2)	
Other main-stem reaches				
Release to PR	13.3 (12.1–15.0)	13.2 (12.0–14.2)	13.4 (11.8–14.7)	NS
PR to WA	33.1 (29.7–36.2)	31.3 (29.1–34.9)	31.4 (28.3–34.8)	NS
WA to RI	31.3 (29.7–33.7)	34.4 (31.0–36.6)	33.4 (29.4–35.9)	NS
RI to RR		37.9 (34.9–40.9)	40.3 (35.9–43.7)	NS
RR to WE		35.3 (33.6–37.5)	39.1 (34.8–42.1)	NS
One-tailed *t*-tests				
Penultimate versus last reach	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	
First versus second reach	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	
2001				
Main-stem reaches adjacent to spawning tributaries				
RI to Wenatchee River	3.7 (2.1–11.2)			
WE to Methow River		3.7 (1.8–7.8)		
WE to Okanogan River			3.0 (1.8–4.8)	
Other main-stem reaches				
Release to PR	12.0 (7.2–14.8)	13.1 (12.4–14.1)	13.7 (12.8–14.7)	NS
PR to WA	38.0 (32.7–42.2)	36.9 (33.9–39.6)	33.7 (30.6–36.8)	NS
WA to RI	29.1 (23.2–38.9)	32.4 (29.4–36.3)	32.8 (25.4–35.2)	NS
RI to RR		45.0 (42.3–48.6)	48.8 (43.2–50.9)	NS
RR to WE		39.9 (37.5–42.5)	43.9 (40.4–46.6)	$P < 0.05$
One-tailed *t*-tests				
Penultimate versus last reach	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	
First versus second reach	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	

Dam and the Methow River confluence (Table 2; $t = -20.6$; df = 82; $P < 0.0001$). Even those fish that slowed the least showed a large and statistically significant reduction in speed. Specifically, in 1999, the Okanogan stock slowed from 39.1 km/d between Rocky Reach and Wells to 19.6 km/d between Wells and the Okanogan confluence (Table 2; $t = -6.1$; df = 36; $P < 0.0001$).

BC Rivers.—Stock differences in summer-run steelhead migration rate were observed in BC rivers. During the 1994 Skeena study, statistically significant differences in migration rate were observed in the reach between the Exchamsiks and Zymoetz junctions (Table 4; $\chi^2 = 13.7$; df = 4; $P = 0.008$), and between the Price and Bulkley junctions (Table 4; $\chi^2 = 14.6$; df = 4; $P = 0.006$). Stock and reach-specific migration data for the Nass River study were sparse, and only two comparisons were possible; no statistically significant stock differences were observed (Table 5; $P > 0.05$).

Similar to the mid-Columbia River fish, those in BC rivers had slow migration rates immediately after release (Tables 4, 5). The result was statistically significant (matched pairs *t*-tests; one tailed *t*-values from 1.9 to 10.8; $P < 0.05$) for all stocks except for Sustut in 1995, for which the sample size was only three fish ($t = 2.4$; df = 2; $P = 0.07$).

The tendency for individuals to slow down in the main-stem reach adjacent to the tributary in which they would eventually spawn was observed, but it was not consistent across all stocks and years (Table 4). The Babine stock slowed down significantly in both years. The Bulkley stock slowed significantly in 1994 but was faster in 1995. The Kispiox stock slowed down in both years, with statistical significance evident only in 1995. In 1994, many of the radio-tagged Kispiox steelhead were not detected by at least one of the last detection zones, hence the sample size for the matched-pairs analysis was only four fish. Nass River stocks could not be included in this analysis due to the pooling of sometimes geographically remote stocks into groupings that covered large portions of the river and several different tributaries.

Comparisons among rivers.—On average, summer-run steelhead traveled through the reaches of the mid-

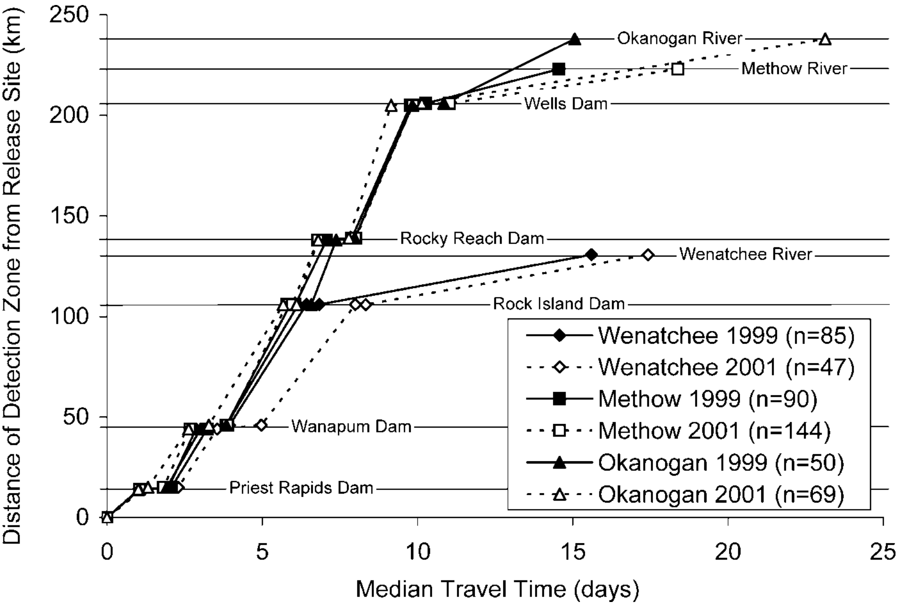

FIGURE 2.—Stock-specific median travel time to each of the detection zones in the mid-Columbia River. The data associated with each detection zone (locations indicated by horizontal lines) are plotted along the *y*-axis by the distance of the detection zone from the release site. Slopes are related to migration rate (i.e., steeper slopes indicate faster migration rates). The migration rates between any two zones are shown in Table 2.

Columbia significantly faster (36.6 km/d; $n = 1,672$) than those traveling through BC river reaches (14.2 km/d; $n = 248$; $\chi^2 = 491.6$; df = 1; $P < 0.0001$). To avoid problems associated with the among-stock differences in sample size, the analysis was repeated, lending equal weight to all stocks within a given river reach. Specifically, the median migration rates (from Tables 2, 4, and 5 under the heading "Other Main-Stem Reaches," excluding rates between the release site and the first upstream detection zone) were used as the dependent variable. The results were very similar. On average, mid-Columbia River fish traveled at median rates of 36.4 km/d, which was significantly faster than BC summer-run steelhead (15.5 km/d; $F_{1,46} = 132.5$; $P < 0.0001$).

Given the relatively fast within-reach migration rates (Table 2) of mid-Columbia River steelhead, coupled with their relatively short dam passage times (Table 3), it followed that migration rates for the mid-Columbia River as a whole (i.e., from below Priest Rapids to above Wells dams) would also be relatively fast. Even when the slowing effects of dams were included in the mid-Columbia River migration rates, mid-Columbia River summer-run steelhead migration rates were still

TABLE 3.—Median dam passage times (h) by stock and dam in 1999 and 2001. Numbers in parentheses are 95% confidence bounds. Chi-square tests test for differences in passage times among stocks; NS = not significant.

Dam	Wenatchee stock	Methow stock	Okanogan stock	χ^2
		1999		
Priest Rapids	20.3 (10.0–23.0)	22.2 (16.7–29.0)	19.6 (14.2–23.9)	NS
Wanapum	9.7 (7.7–16.1)	10.2 (7.7–13.0)	7.6 (5.1–17.4)	NS
Rock Island	5.0 (3.5–6.5)	4.1 (3.3–5.0)	4.5 (4.0–6.6)	NS
Rocky Reach		14.8 (10.3–20.4)	12.3 (8.7–17.4)	NS
Wells		13.0 (10.1–17.7)	13.4 (6.6–27.7)	NS
		2001		
Priest Rapids	15.1 (10.1–27.4)	14.6 (10.8–18.5)	10.3 (6.6–15.7)	$P < 0.05$
Wanapum	20.8 (13.6–36.8)	17.2 (13.1–22.1)	17.4 (10.2–23.3)	NS
Rock Island	8.4 (4.3–13.2)	5.1 (4.3–6.1)	4.9 (3.6–6.9)	NS
Rocky Reach		15.0 (12.0–19.2)	17.4 (12.5–22.8)	NS
Wells		20.8 (15.6–25.6)	23.0 (12.6–30.0)	NS

TABLE 4.—Median migration rates (km/d) by Skeena River steelhead stock and river reach, 1994 and 1995. Numbers in parentheses are 95% confidence bounds. For stocks with sample sizes too low to generate meaningful confidence bounds, the range of observed values is provided in brackets. Chi-square and *t*-tests are as in Table 2.

	Upper Skeena stocks			Middle Skeena stocks		
Reach and *t*-test	Kispiox	Babine	Sustut	Bulkley	Morice	χ^2
		1994				
Reaches adjacent to spawning tributaries						
Skeena–Bulkley junction to Skeena–Kispiox junction	1.5 (1.0–9.1)					
Skeena–Bulkley junction to Skeena–Babine junction		16.0 (9.2–20.3)				
Skeena–Babine junction to Skeena–Sustut junction			17.7 (8.7–23.9)			
Bulkley–Suskwa junction to Bulkley–Toboggan junction				2.9 (1.7–10.6)		
Bulkley–Toboggan junction to Bulkley–Morice junction					6.5 (4.3–18.1)	
Other main-stem reaches						
Ocean release to Skeena–Exchamsiks junction	6.9 (3.1–12.7)	5.1 (4.0–8.2)	7.5 (4.7–9.5)	5.3 (4.1–7.7)	6.0 (3.0–7.6)	NS
Skeena–Exchamsiks junction to Skeena–Zymoetz junction	10.5 (5.4–15.0)	10.7 (6.4–15.3)	16.7 (11.9–18.6)	12.0 (8.7–16.9)	22.6(14.8–23.3)	$P < 0.01$
Skeena–Zymoetz junction to Skeena–Price junction	11.0 (8.5–17.7)	20.3 (10.2–22.0)	19.9 (8.4–25.8)	17.9 (12.3–23.7)	21.6 (12.1–22.5)	NS
Skeena–Price junction to Skeena–Bulkley junction	5.0 (2.1–15.0)	23.0 (7.2–25.5)	21.7(15.7–24.1)	22.2 (12.2–23.4)	28.5 (16.2–35.9)	$P < 0.01$
Skeena–Bulkley junction to Skeena–Babine junction			13.8 (9.7–16.8)			
Skeena–Bulkley junction to Bulkley–Suskwa junction				12.6 (8.5–17.8)	15.6 (12.6–17.6)	NS
Bulkley–Suskwa junction to Bulkley–Toboggan junction					6.9 (5.6–12.1)	
One-tailed *t*-tests						
Penultimate versus last reach	NS	$P < 0.05$	NS	$P < 0.01$	NS	
First versus second reach	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.001$	$P < 0.01$	
		1995				
Reaches adjacent to spawning tributaries						
Skeena–Bulkley junction to Skeena–Kispiox junction	8.6 (0.9–13.5)					
Skeena–Bulkley junction to Skeena–Babine junction		12.3 (7.5–16.2)				
Skeena–Babine junction to Skeena–Sustut junction			21.0 (13.1–24.8)			
Bulkley–Suskwa junction to Moricetown				14.7 (2.7–17.9)		
Other main-stem reaches						
Fish wheel release to Skeena–Price junction	4.1 (4.0–9.2)	6.8 (4.6–9.0)	8.0 (7.3–17.3)	6.2 (3.3–12.5)		NS
Skeena–Price junction to Skeena–Bulkley junction	17.1 (6.6–22.4)	18.5 (14.9–22.7)	22.4 (19.9–27.1)	9.7(2.8–21.3)		$P < 0.05$
Skeena–Bulkley junction to Skeena–Babine junction			12.8 (9.9–21.8)			
Skeena–Bulkley junction to Bulkley–Suskwa junction				5.8 (3.2–9.9)		
One-tailed *t*-tests						
Penultimate versus last reach	$P < 0.05$	$P < 0.0001$	NS	NS		
First versus second reach	$P < 0.05$	$P < 0.0001$	NS	$P < 0.05$		

significantly faster than those of steelhead in similarly large stretches of BC rivers (Figure 3; $\chi^2 = 42.9$; df = 4; $P < 0.0001$). The mid-Columbia River migration rates (19.9 km/d in 1999 and 20.0 km/d in 2001) were significantly faster than those for the Skeena River $\chi^2 = 20.4$; df = 1; $P < 0.0001$). In turn, Skeena migration rates (Price Creek to Bulkley: 15.9 km/d in 1994, 15.5 km/d in 1995; Exchamsiks to Bulkley: 11.9 km/d in 1994) were significantly faster than those observed on the Nass (3.7 km/d; $\chi^2 = 28.3$; df = 1; $P < 0.0001$).

Upstream migration rates of summer-run steelhead were significantly and negatively correlated with river

TABLE 5.—Median migration rates (km/d) by Nass River steelhead stock and river reach, 1993. See Tables 2 and 4 for additional details.

Reach and *t*-test	Lower Nass stocks	Mid-Nass stocks	Upper Nass stocks	χ^2
Main-stem reaches				
Fish wheels to Grease Harbour	1.6 (1.0–2.2)	0.9 (0.5–2.0)	1.3 (1.1–2.0)	NS
Grease Harbour to Nass–Cranberry junction	7.7 (7.2–8.1)	3.8 (0.6–6.6)	4.2 (3.0–7.4)	NS
Nass–Cranberry junction to Nass–Bell-Irving junction			5.9 (4.7–7.9)	
Nass–Bell-Irving junction to Nass–Kwinageese junction			26.1 (16.6–34.6)	
Nass–Kwinageese junction to Nass–Damdochax junction			6.1 (3.2–16.9)	
One-tailed *t*-test (first versus second reach)	$P < 0.05$	$P < 0.05$	$P < 0.01$	

gradient (Figure 3; $r^2 = 0.95$; $F_{1,4} = 77.5$; $P = 0.0009$). There was also a significant positive relationship ($r^2 = 0.69$; $F_{1,4} = 8.8$; $P = 0.041$) with reach location (as the rkm of the downstream boundary of the river reach in which migration rate was measured; Figure 3). The multiple regression was statistically significant ($F_{3,2} = 975.8$; $P = 0.0010$) and explained a large portion of the variation in the data ($r^2 = 0.999$). River gradient was the most important factor in the model ($F_{1,2} = 910.4$; $P = 0.0011$) as the r^2 value of the model excluding this factor was 0.689. Reach location was also a statistically significant effect ($F_{1,2} = 131.4$; $P = 0.0075$; r^2 excluding it = 0.954). When the effects of river gradient and reach location were taken into account, impoundment was still a statistically significant factor influencing the upstream migration speeds of summer-run steelhead ($F_{1,2} = 34.4$; $P = 0.028$), although it was relatively less important to the model than the other factors (r^2 excluding impoundment was 0.988). Travel through the impounded mid-Columbia River was significantly faster than through naturally flowing BC rivers.

Downstream Migration Behavior

Downstream migration speed was estimated for all kelting radio-tagged steelhead that had been tracked to a known tributary spawning ground. Using large, representative river reaches, kelting speed was compared for Skeena (1994 $n = 34$; 1995 $n = 17$), Fraser ($n = 8$) and mid-Columbia River (2001 $n = 23$) steelhead. Median downstream migration rate for mid-Columbia River steelhead kelts (12.8 km/d) was significantly slower ($\chi^2 = 23.8$; df = 1; $P < 0.0001$) than that for BC steelhead. Fraser steelhead median kelting speed (99.8 km/d) was significantly faster than that for Skeena steelhead ($\chi^2 = 4.4$; df = 1; $P = 0.035$). Skeena kelting speed was not significantly different between study years (42.3 km/d in 1994; 54.3 km/d in 1995; $\chi^2 = 0.58$; df = 1; $P = 0.45$).

Downstream migration speeds for kelts were not correlated with river gradient ($r^2 = 0.006$; $F_{1,2} = 0.01$;

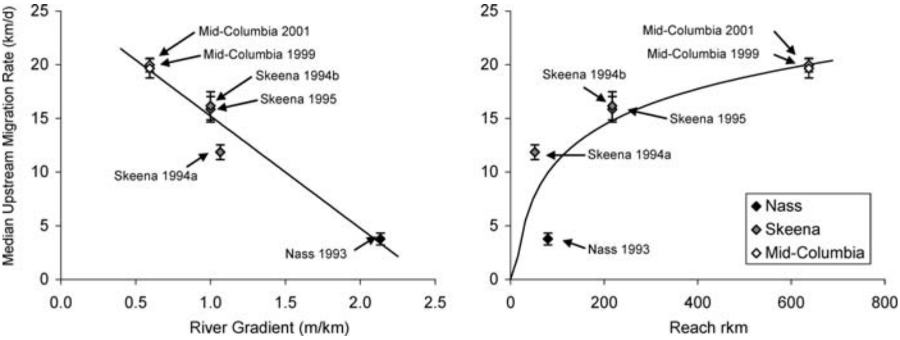

FIGURE 3.—Median upstream migration rates by river gradient and reach location (i.e., from the downstream boundary of the river reach in which the migration rate was measured) for steelhead in the Nass, Skeena, and mid-Columbia rivers. Migration rates are the means of 1,000 medians, bootstrapped from the raw data; error bars show the standard deviations of the 1,000 medians. A representative river reach was selected for each study so as to be as large as possible while still encompassing the majority of the fish. The Columbia River reach extended from the Priest Rapids Dam tailrace to the Wells Dam forebay. Two Skeena River reaches were used in 1994: (a) from the Exchamsiks River junction to the Bulkley River junction and (b) from Price Creek to the Bulkley River junction; the latter was used in 1995. The Nass reach was from Grease Harbour to the Cranberry River junction. The most direct comparison of Skeena studies is between 1994b and 1995, as both are based on travel through the same reach.

$P = 0.92$) or tagging location ($r^2 = 0.15$; $F_{1,2} = 0.35$; $P = 0.62$).

Discussion

Summer-run steelhead in the mid-Columbia River traveled upriver faster than those in naturally flowing BC rivers. Fast swim speeds were likely possible in the mid-Columbia because of a weak river gradient, lower water velocities that result from impoundment, and fishways that were effective at facilitating movements of anadromous fish past the vertical ascents associated with dams. The location of the study area, which was 639 km from the river mouth, also appeared to influence measured migration rates.

River gradient was the most important factor explaining the variation in upstream migration rates among rivers. This was not surprising as steeper gradients are associated with stronger currents and faster flowing water. When fighting a current, increased energy is required to maintain speed over ground, and travel times decrease relative to those in more lentic areas. River current can influence upstream migration rates, swimming speed and path selection in salmonids (Standen et al. 2004), and more energy is expended in areas of higher velocity (Standen et al. 2002). Although it is relatively difficult to collect data on the velocities encountered by fish in large, complex river systems, especially over long distances (Keefer et al. 2004), river gradient was used in this study as a simple proxy since it was easily measured, and it integrated velocity over the river segment in question.

The upstream migration rates measured in this study were not independent of the location at which they were measured. For among-river comparisons, migration rates were faster in the studies where the measurements were made relatively far from the ocean, and were slower than in the studies done farther downstream. Migration rates in two overlapping reaches were measured in the Skeena River in 1994, and the same trend was observed. Movements through the long reach (which included the lower parts of the river) were significantly slower than those through the shorter reach (which was restricted to the upper river). The results in Table 4 showed that the trend was consistent for most of the stocks migrating through the common reaches along the Skeena main stem in 1994. Spence (1989) found similar results for Skeena River steelhead in 1988, and the migration rates were nearly identical to those in our study (Table 4).

Within-river speed changes were not limited to the Skeena River. In the lower Columbia River, steelhead migration rates between Bonneville (rkm 235) and McNary (rkm 470) dams were slower than those between Bonneville and Priest Rapids dams (Keefer et al. 2004), indicating that speed increased as the fish moved upriver. This study showed that migration rates increased further as fish moved into the mid-Columbia upstream of Priest Rapids Dam. Similarly, Nass steelhead increased in speed as they moved upriver along the main stem of the river (Table 5). For all these comparisons, data from each individual's terminal river reach were excluded to avoid measuring the slowing effects observed near spawning tributaries.

Steelhead reduced migration speeds in main-stem reaches adjacent to their spawning tributary. In this study, mid-Columbia River steelhead and some Skeena River stocks slowed down significantly in their final main-stem reach. Spence (1989) observed the same trend for Skeena River steelhead in 1988. The reduced migration rates could have resulted from several different steelhead behaviors. For example, fish could respond to changing levels of olfactory stimuli (e.g., Hasler and Scholz 1983), and reduce speed in order to locate the tributary's mouth. Alternatively, slow migration rates could be the result of fish holding in main-stem reaches adjacent to spawning areas when water levels or temperatures in the destination tributaries are not suitable for migration, overwintering or spawning. Alexander et al. (1998) found that salmonids held in main-stem areas until the tributary water cooled to more suitable temperatures, at which time a large-scale ingress event was observed. Lough (1983) found similar delays, but attributed them to changes in water level rather than temperature. Adult steelhead were observed holding in main-stem pools along the Upper Nass River for several weeks in 1993 when water levels in the Damdochax River were unusually low (Alexander and Koski 1995). In Lake Michigan, temperature was shown to be an important factor stimulating upstream migratory movements, and stream flows were less important (Workman et al. 2002). Our study occurred at the time of year when mid-Columbia River tributary temperatures could have been cooling and water levels dropping from their summer peaks. However, a synchronized mass-ingress of steelhead was not observed. A third possibility is that fish overshot their spawning tributary and had to spend extra time back-tracking. This additional time would result in slower migration rates through their last main-stem reach.

Impoundment resulted in increased upstream swim speeds of mid-Columbia River steelhead. When river gradient and reach location were controlled, a multiple regression indicated that impoundment was, nevertheless, a statistically significant factor. That is, impoundment resulted in significantly faster upstream swim speeds than would have been observed in naturally flowing rivers of similar gradient, and of similar distance from the river mouth. In this study, delays associated with dam passage were short, and were more than compensated for by the rapid movements between dams. Keefer et al. (2004) saw a similar pattern in dam and reservoir travel times for steelhead in the lower Columbia and Snake rivers.

Impoundment affects steelhead migration rates in several ways. Impoundment has altered the Columbia River discharge regime, resulting in a flattening of the hydrograph. Relative to historical rates, the summer flows have dropped and those during other times of the year have increased (National Research Council 2004). Decreased summer flows would tend to increase migration rates of summer-run fish. Secondly, the lentic reservoirs that form behind dams likely offer less resistance to upstream migrants than a naturally flowing river. In fact, the majority of the vertical ascent in the mid-Columbia River is experienced within the fishways of the dams. The fishways, controlled environments designed to allow the movement of salmonids past the dam, have negligible year-to-year variation in flow. This probably explains why the migration rates estimated for mid-Columbia River summer-run steelhead showed little annual variation despite substantial differences in river flow (3,760 m^3/s in 1999; 1,925 m^3/s in 2001). Similarly for the lower Columbia and Snake rivers, Keefer et al. (2004) found that year-to-year variation in discharge was not strongly related to upstream migration rates.

Temperature and latitude were not included in the multiple regression due to their collinearity with gradient (temperature–gradient $r^2 = 0.98$). The more northern (higher latitude) rivers in our studies had the steepest gradients and lowest temperatures. Consequently, we could not separate the effect of temperature and latitude from those of gradient. Water temperature is nevertheless a potentially important factor affecting steelhead distribution and migration (Baigún et al. 2000; Robards and Quinn 2002; Höök et al. 2004), especially within years. For example, Keefer et al. (2004) found that steelhead upstream migrations slowed dramatically when summer water temperatures peaked, then increased as rivers cooled in fall. Similar observations have been reported for Okanogan sockeye salmon *O. nerka* migrating through the main-stem reach on the mid-Columbia River above Wells Dam (Alexander et al. 1998). In both of these Columbia River studies, peak water temperatures were much higher than those observed in the more northern rivers.

Downstream (kelting) migration speeds, compared across river systems, were not found to be a function of gradient or river kilometer. However, Hatch et al. (2003) reported increasing kelting speeds as fish approached the mouth of the Columbia River. Steelhead kelting from March to June 2002 had traveled at 14.4 km/d through the Snake River between Lower Granite and Ice Harbor dams; and increased speed to 35.7 km/d when traveling through the lower Columbia River from Ice Harbor to Bonneville dam. One might expect that the mid-Columbia River kelting speeds observed in this study (12.8 km/d) would have increased if telemetry coverage had extended into the lower river. Nevertheless, the mid-Columbia River kelting speeds were significantly slower than those on free-flowing BC rivers, likely as a result of the lentic qualities of the reservoirs behind each dam, and perhaps dam passage. Fraser steelhead kelting speed was fastest, likely a result of the large water volume, which is sometimes confined and hence of high velocity (e.g., Hell's Gate) during the spring out-migration. The proportion of spawners that kelted was significantly higher for spring and winter-run steelhead than for summer and fall runs, likely due to their much shorter period of freshwater residence before spawning.

Several capture methods were used in the seven studies under consideration. However, the studies were designed without inter-study comparisons in mind and capture method was not fully replicated within each river or within each run-timing group. Angling and tangle netting methods were used only for spring, winter and fall-run steelhead on the Bella Coola and Fraser rivers; and purse seines, fishwheels, and traps were used only on summer-run steelhead on the Skeena, Nass and mid-Columbia rivers. As such, effects associated with run-timing cannot be separated from those associated with capture methodologies or river system.

Many of the radio-tagged fish, possibly stressed from handling, drifted downstream after release. Such post-tagging downstream movements have been observed by other authors (e.g., Mäkinen et al. 2000 and references therein). In some studies, telemetry receivers were deployed downriver of the release site in order to detect downstream movements. However, postrelease effects could be detected in all studies, regardless of the receiver deployment because estimates of migration rate between the release site and the first upstream detection zone were significantly slower than subsequent migration rates for all stocks in all rivers in all years (except for the Sustut stock in 1995, which had a sample size of only three fish). Alexander et al. (1996) found that holding time affected the probability of downstream movements post tagging. Steelhead that spent more than 10 h in the fishwheel holding pen before being tagged were more likely to drift downriver than those that were in the holding pen for less than 10 h

The proportion of fish that survived the handling process was significantly greater for fall-, winter-, and spring-run steelhead than for summer-run steelhead. It is possible that elevated summer water temperatures increased the stress associated with the tagging experience. Fish in water that is closer to their upper thermal limit (approximately 25 degrees for *O. mykiss*, Threader and Houston 1983) experience higher levels of "background" stress (Dawson 1992) and may be more vulnerable to mortality from additional stressors (e.g., Holt et al. 1975). It is possible that some individuals capable of surviving the tagging process in cool water would not survive when tagging stress is combined with that from being held in warm water. In this study, the average temperatures during tagging of summer-run stocks ranged from 10 to18°C; whereas that for the tagging of nonsummer-run stocks was 3–11°C.

More mid-Columbia River steelhead survived the tagging process than is apparent from the ϕ_1 metric. The release site for the mid-Columbia studies was immediately upstream from known spawning areas in the Hanford Reach (Becker 1985), and from the Yakima River (a known spawning tributary, Tuck 1994). The mid-Columbia River release site was also only 104 km upstream from the junction of the Snake River, a relatively important steelhead spawning river (Beacham et al. 2004). These three spawning areas accounted for 8.6% of the steelhead captured and tagged at Priest Rapids Dam. It is probably incorrect to relate the downstream migration of these fish to tagging effects.

The location of the fixed station receivers probably did not bias the ϕ_1 analyses. The receiver closest to the tagging location (in the downstream direction) was between 2 and 24 km in all studies except for the Fraser, where the fall angling in 1996 occurred 62 km from the nearest downstream receiver. Excluding the Fraser River fall angling in 1996 did not change the reported result. There was no correlation between the ϕ_1 values and the downstream receiver distances ($r = 0.03$; $P = 0.93$).

The proportion of fish tracked to upstream spawning areas (i.e., the tracking and migration success, ϕ_2) was consistently high for summer-run steelhead. No significant differences could be detected among studies involving summer-run steelhead; however, the statistical power was weak because of small sample sizes.

In conclusion, this study provides the first published upstream and kelting migration rates for steelhead in the major rivers of the Pacific Northwest. The upstream migration rates were best explained by river gradient and distance of the study area from the ocean. However, when the effects of river gradient and reach location were taken into account, impoundment was still a significant factor increasing the upstream migration speeds of summer-run steelhead. Kelting speeds varied widely among rivers and did not appear to be a function of gradient.

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