Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat

Joseph H. Anderson and Thomas P. Quinn

Abstract: Pacific salmon (*Oncorhynchus* spp.) have repeatedly exploited new habitat following glacial recession and some artificial introductions, yet the initial process of colonization is poorly understood. Landsburg Diversion Dam on the Cedar River, Washington, excluded salmon from 33 km of habitat for over a century until it was modified to allow passage in 2003. Adult coho salmon (*Oncorhynchus kisutch*) were sampled as they entered the newly accessible habitat in the first 3 years and a subset received radio transmitters to assess spawning site selection and movement. Annual counts of coho colonists increased over time, and in 2 of 3 years, daily dam passage was positively correlated with river discharge. Contrary to our prediction that coho would spawn in tributaries, all identified spawning sites were in the mainstem Cedar River, though 38% of radio-tagged salmon entered a tributary at least temporarily. Females moved little within the new habitat (average = 5.8 km), whereas males moved extensively (average = 34.8 km), especially when females were scarce. The immediate use of the new habitat by colonists and their widespread movements suggest that exploration is an innate component of salmon breeding behavior, and restoring access to lost habitat merits prioritization as a conservation strategy.

Résumé : Après le retrait des glaciations et à la suite d'introductions artificielles, les saumons du Pacifique (*Oncorhynchus* spp.) ont exploité de façon répétée de nouveaux habitats; néanmoins, le processus initial de colonisation reste peu compris. Le barrage de dérivation Landburg sur la rivière Cedar, Washington, a exclu les saumons d'un habitat de 33 km pendant plus d'un siècle jusqu'à ce qu'il soit modifié en 2003 pour permettre leur passage. Les saumons coho (*Oncorhynchus kisutch*) ont été échantillonnés durant les 3 premières années après leur pénétration dans l'habitat nouvellement disponible; un sous-ensemble de ces poissons ont été munis de transmetteurs radio afin de déterminer leur choix de site de fraye et leurs déplacements. Les dénombrements annuels de saumons coho colonisateurs se sont accrus avec le temps et dans 2 des 3 années leur passage journalier au barrage était en corrélation positive avec le débit de la rivière. Contrairement à notre prédiction que les saumons coho frayeraient dans les tributaires, tous les sites de fraye identifiés se situent dans le cours principal de la rivière Cedar, bien que 38 % des saumons munis d'une étiquette radio ait pénétré au moins temporairement dans un tributaire. Les femelles se déplacement peu dans le nouvel habitat (moyenne = 5,8 km), alors que les mâles se déplacent beaucoup (moyenne = 34,8 km), particulièrement lorsque les femelles sont rares. L'utilisation immédiate du nouvel habitat par les colonisateurs et leurs déplacements étendus indiquent que l'exploration est une composante innée du comportement de fraye des saumons; il y a donc intérêt à restaurer l'accès aux habitats perdus comme stratégie prioritaire de conservation.

[Traduit par la Rédaction]

Introduction

Habitat colonization is critical to population biology, as a species' range reflects the countervailing forces of colonization and local extinction. Strict philopatry (i.e., homing to the natal site for reproduction) precludes exploration and possible colonization of new breeding areas. It is unclear whether colonization results from orientation failure or active exploration of new areas despite properly functioning homing mechanisms. Orientation failure may place colonists into new habitats over a range of distances from the source

population. Alternatively, non-natal spawning sites with more favorable environmental conditions or reduced competition may attract breeders to explore and colonize new areas, though this process may operate over shorter distances than orientation failure. Indeed, a population must contain at least a small proportion of exploratory rather than philopatric spawners to ensure long-term population viability (LePage and Cury 1997). Exploratory behavior is of immediate significance to a population because homing by the offspring of colonists permits new breeding areas to become established in a single generation (Cury 1994). By describ-

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ing the behavior of colonizing individuals, we can understand mechanisms of population dispersal and its significance to population structure (Rieman and Dunham 2000).

Homing to the natal spawn site is a hallmark of salmonid fishes such as Pacific salmon (*Oncorhynchus* spp.), yet some "strays" survive to maturity and spawn away from their natal site (Quinn 1993). Homing, combined with generations of natural selection, leads to the evolution of traits advantageous to local conditions (Ricker 1972; Taylor 1991; Quinn 2005). However, strays are important to the evolutionary plasticity and geographic distribution of the species, as they allow for colonization of new habitat. Both postglacial history and experience with transplanted populations illustrate that salmon can exploit open habitat. Salmon expanded into areas made available by receding glaciers from northern Washington to southern Alaska and proliferated in a myriad of geologically young streams (McPhail and Lindsey 1986). This colonization process continues in regions of glacial recession such as Glacier Bay, Alaska, where salmon colonization follows development of complex stream habitat (Milner and Bailey 1989; Milner et al. 2000). Further evidence for the colonization potential of Pacific salmon comes from artificial introductions outside their native ranges, including pink salmon, *O. gorbuscha*, in the Great Lakes (e.g., Kwain 1987) and Chinook salmon, *O. tshawytscha*, in New Zealand (e.g., Quinn et al. 2001) and Argentina (Ciancio et al. 2005). In each case, salmon rapidly dispersed into nearby unoccupied streams and established self-sustaining populations. Unfortunately, the initial stages of these colonization events are shrouded in the past, and processes occurring at the onset of colonization are not well understood.

Furthermore, we know little about the factors promoting successful colonization. We postulate that success might depend on three behavioral processes: (*i*) entry into the new habitat, (*ii*) exploratory movements before breeding, and (*iii*) selection of spawning sites. Research on entry into new habitat should document the basic attributes of salmon colonists (e.g., abundance, seasonal timing, sex, body size, and origin, including whether the fish were produced naturally or in a hatchery) as population expansion proceeds through time and the environmental conditions affecting upriver movement into new areas. Hydrologic conditions might be particularly important, as upriver movement of salmonids is often triggered by increased discharge in small streams (Banks 1969). Although the effects of water temperature on upriver movement are variable (Banks 1969), salmonids avoid extremely warm areas during spawning migrations (Berman and Quinn 1991; Newell and Quinn 2005).

Colonization may result from a breakdown of olfaction and homing to the natal site (Dittman and Quinn 1996), from active choice of a non-natal breeding area, or from some combination of the two. Thus exploration and spawning site selection are important components of colonization behavior. Females need to locate suitable breeding sites because they alone prepare nests, so movement and spawning site selection are intimately linked. Coho salmon, *Oncorhynchus kisutch*, for example, tend to use small tributaries for breeding (Sandercock 1991; Montgomery et al. 1999; Quinn 2005), and densities of juvenile coho salmon are also typically highest in tributaries of larger rivers (Rosenfeld et al. 2000; Scarnecchia and Roper 2000), although some rear in mainstem sections of rivers (Peters 1996). During the early stages of colonization, densities will presumably be low relative to established populations, and female salmon may not be restricted by competition for spawning sites (e.g., van den Berghe and Gross 1989), or by homing to the natal site, and thus female movements may directly reflect choice of breeding habitat.

Movements of adult salmon vary according to stage of sexual maturation, as migrating salmon behave differently than spawning salmon. Migrating salmon can move rapidly (Keefer et al. 2004) and may show a "search phase" prior to spawning characterized by erratic upstream and downstream movements, presumably as they search for natal odors or select breeding habitat (Økland et al. 2001; Connor and Garcia 2006). In large rivers, these search movements cover long distances (Keefer et al. 2006). However, there have been fewer studies of adult salmon movements on the spawning grounds, and the results have been mixed. Movement by males may be determined by the distribution of ripe females in both space and time. Radio tracking revealed considerable movement by male coho salmon, likely in search of mates (Healey and Prince 1998), but spawning ground movements of male sockeye salmon (*Oncorhynchus nerka*) experiencing much higher intraspecific breeding densities were very limited (Hendry et al. 1995; Stewart et al. 2004; Rich et al. 2006).

The construction of a fish ladder by Seattle Public Utilities at Landsburg Diversion Dam on the Cedar River, Washington (Fig. 1), presented a rare opportunity to investigate the process of salmon colonization. The ladder, completed in fall 2003, made 33 km of suitable spawning habitat accessible to Chinook salmon, coho salmon, and steelhead trout (*Oncorhynchus mykiss*) that had been excluded since the dam was constructed in 1900. The newly available habitat includes the mainstem Cedar River and four tributaries, of which Rock Creek offers the majority of potential salmon habitat (accessible area with moderate gradient, woody debris, and a mixture of pools and riffles).

To investigate the process of colonization, adult coho salmon were sampled as they passed Landsburg Diversion Dam, and some were radio-tracked to characterize their movements. The study had three principal objectives. First, we recorded basic demographics of colonists entering the new habitat: abundance, timing, body size, and origin (hatchery or naturally spawned). Dam passage data were secondarily used to evaluate the proximate environmental stimuli for upriver movement into the newly accessible area. Second, we assessed reach-scale patterns in spawning site selection, hypothesizing that coho salmon would spawn primarily in tributaries, especially Rock Creek, rather than the mainstem Cedar River. Third, we determined the effects of river discharge, date, body size, and access to breeding opportunities on the movements of individual salmon in the newly accessible habitat. We compared the movements of females having access to a large number of potential breeding sites with those of males having access to a small number of possible mates. Our analysis tested the hypothesis that salmon movements would be inversely related to breeding opportu-

nity: males would be more mobile than females, and males would be more mobile when reproductively active females were scarce.

Materials and methods

Study site description

The Cedar River drains a 487 km^2 watershed in Washington State, flowing westward from the crest of the Cascade Mountains (Fig. 1) into the southern end of Lake Washington, and then to marine waters via a shipping canal. In 1900, the City of Seattle constructed Landsburg Diversion Dam, a low head, run-of-the-river facility, at river kilometre 35.1 to supply Seattle residents with drinking water. This dam blocked salmonid migration until passage facilities were completed in fall 2003, making available over 33 km of habitat in the mainstem Cedar River and tributaries. Much of the landscape is dominated by second-growth coniferous forest aged at least 60 years (Seattle Public Utilities 2000), and the City of Seattle now manages the area above Landsburg Diversion Dam as a de facto reserve, without development, recreation, or commercial logging. Coho salmon spawn naturally in the Cedar River and tributaries below Landsdsburg Diversion Dam, although no comprehensive population estimates were available. In contrast to the upper watershed, land use of the Cedar River watershed below the dam is dominated by suburban development.

Of the 33 km of new habitat now accessible to salmon, 20 km are located in the Cedar River between Landsburg Diversion Dam and lower Cedar Falls, a natural barrier to migration. The Cedar River has a relatively confined channel, and densities of instream large woody debris are lower than in similar streams in western Washington (Kiffney et al. 2002). The remaining 13 km of newly accessible habitat are found in the tributaries (Rock, Williams, Steele, and Taylor creeks). Only very short sections (<0.5 km) of Williams, Steele, and Taylor creeks are accessible to salmon before they are blocked by natural barriers. The majority of tributary habitat available to salmon is in Rock Creek, which is also the first tributary that a salmon would encounter swimming upriver from the Landsburg fish passage facility. For these reasons, much of the radio-tracking effort was directed to Rock Creek.

In addition to salmon, the Cedar River watershed below Cedar Falls contains resident fish typical of many streams in western Washington. Salmonid species include rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarkii*), and mountain whitefish (*Prosopium williamsoni*). In general, trout densities are much lower in the Cedar River than in rivers of comparable size in western Washington (Kiffney et al. 2002). Nonsalmonid fishes in Cedar River and tributaries include speckled dace (*Rhinichthys osculus*), brook lamprey (*Lampetra richardsoni*), and several sculpin species (*Cottus* spp.) that are numerically dominant.

Movement through the fish passage facility

Adult coho salmon were sampled as they moved upriver through the fish passage facility at Landsburg Diversion Dam. For the great majority of the run, a gate prevented salmon from accessing the new habitat unless they were

Fig. 1. Map of Cedar River watershed above Landsburg Diversion Dam (Washington, USA). Broken lines represent habitat that is inaccessible to salmon, as indicated on maps provided by Seattle Public Utilities. Shaded circles and two letter codes refer to the listening stations, where the size of the circle is not proportional to the range of the antennas.
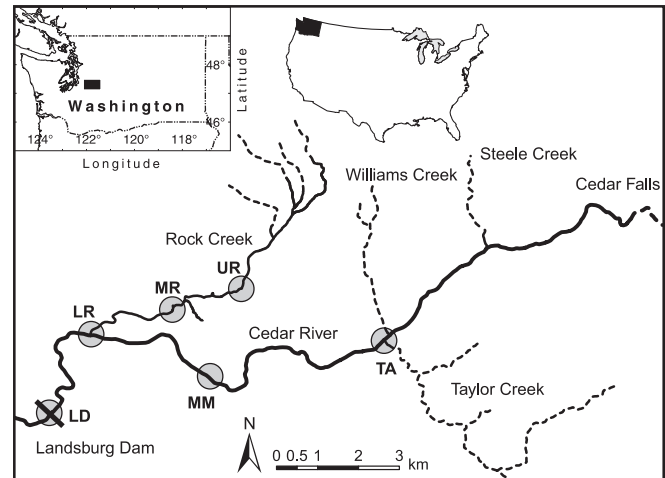
handled. The facility was operated in this mode from before the run began until the run was deemed over (0–1 fish migrating upriver in 2 weeks). The date of passage, species, sex, and length were recorded for each fish. Fork length was measured in 2004 and 2005; total lengths measured in 2003 were converted to fork lengths with data from the nearby University of Washington hatchery using sex-specific linear regressions (males, $n = 28$, $p < 0.0001$, $r^2 = 0.997$; females, $n = 21$, $p < 0.0001$, $r^2 = 0.987$). The fish were also examined for the presence or absence of an adipose fin as an indication of natural spawning or hatchery origin, respectively. In the brood years that returned during this study, virtually all hatchery-produced coho salmon were adipose-clipped at the two hatcheries in the basin producing this species (Issaquah Creek and University of Washington). After the fish passage gate was opened late in each season, a few salmon might have passed upriver unsampled but an automatic camera indicated that unsampled fish were <5% of the total run in any year.

Generalized least squares (GLS) regression models were used to determine the relationship between upriver movement past Landsburg Diversion Dam and both temperature and discharge, recorded at US Geological Survey gauges located within 3 km of the dam. The data used were from 1 week before the first upriver movement through the ladder to 1 week after the last upriver movement in each season ($n = 90$ days in 2003, 130 days in 2004, and 121 days in 2005). With adult counts as the response variable, regression explored four predictor variables: mean daily discharge (Q), change in discharge from the previous day (ΔQ_{t-1}), mean daily temperature (T), and change in temperature from the previous day (ΔT_{t-1}). Environmental and count data were collected on successive days, and a GLS approach considers such data as a times series (Trépanier et al. 1996). The model error structure was specified as a first-order autoregressive process and parameters were estimated via maxi-

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mum likelihood (Ostrom 1990). For the GLS models, listed *p* values are from *t* tests for the significance of each predictor, and we also report Nagelkerke's (1991) adjusted r^2, which compares the log likelihood of the fitted model with the log likelihood of the null (intercept only) model.

Telemetry

Some of the coho salmon bypassing Landsburg Diversion Dam in 2003 and 2004 received radio transmitters via esophageal implant. The transmitters (model F1845, Advanced Telemetry Systems, Inc., Isanti, Minnesota) weighed 24 g in air, with a maximum battery life of 360 days. Movements of radio-tagged fish were determined by listening stations and mobile tracking. Listening stations at strategic locations along the mainstem Cedar River and tributaries continuously scanned for transmitters (Fig. 1) with a receiver–datalogger unit and three antennas positioned to indicate the direction of movement. Four such listening stations were located in the newly accessible habitat in fall 2003: the lower Rock Creek (LR) station was at the confluence with the mainstem; the middle Rock Creek (MR) station was 2.5 km upstream from the Cedar River; and the upper Rock Creek (UR) station was 4.6 km up Rock Creek from the Cedar River. The final station was at the confluence of the Cedar River and Taylor Creek (TA). In fall 2004, two new listening stations were added: one at Landsburg Dam (LD) and another on the middle of the mainstem Cedar River (MM), halfway between Rock and Taylor creeks. The initial distribution of listening stations in 2003 was based on our expectation that coho salmon would spawn primarily in Rock Creek; two stations were added in 2004 in response to movement patterns of the fish in 2003. Listening stations were operational each season until it was clear that all movement had ceased.

Mobile tracking by automobile, foot, and raft helped locate tagged fish between listening stations at two different spatial scales: river sections and exact GPS coordinates. Tag positions from both scales were incorporated into a single analysis of movement, as exact locations were nested within river sections. Automobile surveys described the general distribution of tagged salmon above the dam by assigning fish to discrete river sections bounded by predetermined GPS waypoints. The 27 such surveys in 2003 and 25 in 2004 covered an average of 12.8 km (2003) and 11.8 km (2004) of mainstem and tributary habitat. A handheld GPS unit (GPS 76, Garmin, Inc.) defined the way points, and fish were recorded in one of 44 river sections (average length = 554 m, standard deviation (SD) = 190 m).

Foot surveys augmented the automobile tracking to determine precise tag locations or directly observe salmon, but high turbidity, discharge, and the cryptic coloration of spawning coho salmon made direct observations difficult. Consequently, raft surveys (two in 2003, eight in 2004, and two in 2005, including one survey below Landsburg Diversion Dam in 2003 and 2004) were conducted for radio tracking, observations of redds and salmon, and carcass sampling. Direct observations and transmitter detections were recorded as GPS locations for integration with the other types of positional data. Further details on telemetry survey methods can be found in Anderson (2006).

Telemetry data were used to identify specific behaviors and to quantify the overall movement history of individual

salmon. The behaviors considered were movement into the tributaries and downstream passage over Landsburg Diversion Dam (2004 only). To relate these two types of movement and Cedar River discharge, we used a GLS procedure identical to that described for counts of upriver movement through the fish ladder. To quantify each individual's movements, the telemetry detections from all sources were organized chronologically and the movements between detections were estimated using ArcGIS version 9.1 (ESRI, Inc., Redlands, California; see Anderson (2006) for further details) to provide minimum estimates of total distance traveled. The last downstream movement was not included because this was assumed to be postmortem drift rather than active movement. Ordinary least squares regression was used to explore the relationship between individual movement and a variety of predictor variables, with separate analyses for males and females. More movement was detected in 2004 than in 2003 because there were more listening stations (six vs. four) and more frequent mobile surveys. To facilitate comparisons between years we standardized the data using a formula analogous to the *Z* statistic (Zar 1999):

$$(1) \qquad \text{standardized movement } (x) = \frac{x_i - \bar{x}}{\sigma}$$

where x_i is a movement value for fish i, $\bar{x}$ is the average movement within a year, and σ is the standard deviation of movement within a year. Two types of predictor variables were used to explain movement: phenotypic characters (fish length and date of passage at the dam) and conditions encountered on the spawning grounds, which included river discharge (females and males) and availability of ripe females (males only). Both discharge and female availability were averaged over each individual's days of active movement. To estimate the number of ripe females available to each male, we used the counts of females passed upstream at the ladder and assumed that they would be ripe for 1 week based on observations of sexual maturity at the dam.

Results

Fish passage

The number of adult coho salmon colonizing the new habitat increased each successive year (Fig. 2), and salmon ascended the fish ladder over a protracted period beginning in early October (Fig. 3). In 2003–2004, 47 coho salmon ascended from 7 October to 21 December (median = 29 November). In 2004–2005, 99 coho salmon migrated upriver through the fish ladder from 11 October to 3 February (median = 13 December). In 2005–2006, 170 coho salmon accessed the new habitat from 9 October to 23 January (median = 20 December). In 2004 and 2005, the migration period extended well past that observed in 2003. Structural modifications made between the 2003 and 2004 seasons at the ladder facility improved late-season capture efficiency, so it is unclear whether this difference was an artifact of sampling or reflected an increase in late season migrants (P. Faulds, Seattle Public Utilities, P.O. Box 34018, Seattle, WA 98124, USA, personal communication). In all three seasons, more males than females entered the new habitat (Fig. 2), but the entry date did not differ between sexes within any

Fig. 2. Number of adult coho salmon (*Oncorhynchus kisutch*) entering the newly accessible habitat by year, sex, and origin (i.e., clipped adipose fin indicated hatchery origin). From left to right within each year: hatchery females (hatched bars), hatchery males (solid bars), naturally spawned females (shaded bars), and naturally spawned males (open bars).
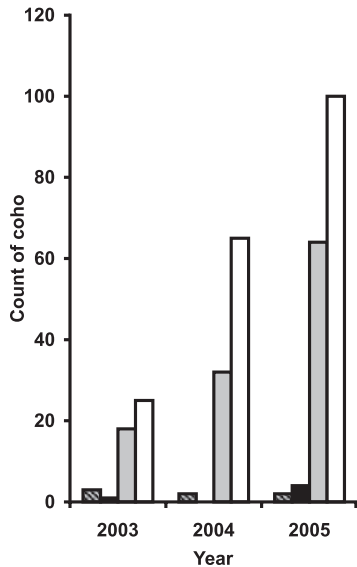
year (*t* tests, $p > 0.05$). Very few coho salmon (3.8% for all years pooled) had clipped adipose fins, indicating that the majority of colonists were naturally produced (Fig. 2). Male size-frequency distributions were unimodal in 2003 and 2004, but in 2005, a second mode below 500 mm fork length likely represented younger, age-2 males, known as jacks (percent of males <500 mm long: 2003, 0.0%; 2004, 1.5%; 2005, 24.0%). Female size-frequency distributions appeared unimodal in all three seasons.

Generalized least squares models revealed that both Cedar River discharge and change in discharge were positively associated with counts at the ladder in 2 of 3 years (discharge: 2003, $p = 0.007$, $r^2 = 0.09$; 2004, $p < 0.0001$, $r^2 = 0.14$; 2005, $p = 0.6$; change in discharge from the previous day: 2003, $p = 0.0001$, $r^2 = 0.16$; 2004, $p = 0.03$, $r^2 = 0.04$; 2005, $p = 0.4$; Fig. 3). Average discharge differed between the years (one-way analysis of variance, ANOVA, $F_{2,338} = 8.0$, $p = 0.0004$), and Tukey tests indicated that 2005 discharges (average = 26.2 $m^3 \cdot s^{-1}$) were higher than those in 2003 (21.0 $m^3 \cdot s^{-1}$, $p = 0.01$) and 2004 (20.0 $m^3 \cdot s^{-1}$, $p = 0.0005$), but discharges in 2003 and 2004 did not differ from each other ($p = 0.8$). Although colder temperatures and higher flows tended to occur toward the end of each season, discharge and temperature were unrelated in a time series regression (GLS, $p > 0.05$). Temperature was not consistently related to upriver movement. In 2003, ladder counts were positively correlated with temperature change from the previous day ($p = 0.002$, $r^2 = 0.11$) but there were no other significant relationships between ladder counts and either temperature or temperature change ($p > 0.05$). Finally, there was little difference in mean temperature between years during the period of coho salmon movement (2003 = 8.3 °C, 2004 = 8.3 °C, 2005 = 7.6 °C; one-way ANOVA, $F_{2,336} = 2.7$, $p = 0.07$).

Spatial distribution patterns

In 2003, 14 females and 23 males received radio tags. In 2004, four females and 45 males received transmitters. In each year, more males were tagged than females, in part because males were more numerous (Fig. 2) and in part because females carried a limited number of gametes and we were concerned that tagging many females may have reduced population productivity through gametes lost via tagging stress. Tagging approximated the overall arrival distribution in 2003, but in 2004, 22 of the 50 fish that did not receive transmitters passed the dam after the final transmitter was implanted, so the tracking data did not represent the latest fish. Nevertheless, the median tagging date matched the median date of all coho salmon passage in both seasons.

Most tagged coho salmon tended to remain in the lower reaches of the Cedar River and few reached Taylor Creek, 12.5 km above the dam (Table 1). In each season, only one individual was detected at the middle Rock Creek site (MR), 2.5 km upstream from the confluence with the Cedar River, and no salmon were detected at the upper Rock Creek (UR) site (Table 1). However, there were many temporary entrances into Rock Creek and two into Taylor Creek (Table 2). Tributary entrances were positively related to discharge in the Cedar River in both years (i.e., entrances were more common when discharge was high; GLS: 2003, $p = 0.003$, $r^2 = 0.10$; 2004, $p = 0.004$, $r^2 = 0.11$). Only two of the 61 entrances were permanent; all others were temporary, and all but four of those were <24 h duration. A higher proportion of males entered tributaries than females (Table 2), and males more often made multiple tributary entrances (Table 2).

All coho salmon redds identified above the dam (5 in 2003, 18 in 2004, and 12 in 2005) were in the Cedar River (almost all in the lower reaches of the newly accessible section), and no redds were in the tributaries. All redds observed in 2003 were <7.0 km from the dam (median = 4.7 km, range = 1.2–6.5 km), as were all but two seen in 2004 (median = 4.8 km, range = 0.9–13.5 km). No radio tracking was conducted in 2005, but surveys of the Cedar River indicated that redds tended to be farther upriver; 50% were >7.0 km above the dam (median = 8.1 km, range = 3.9–12.8 km). Certain areas perennially attracted coho salmon; notably, 31% of all identified redds were in a 700 m section beginning 4.7 km above the dam. Most redds were along the margins of the river, often within 5 m of the bank, and the wetted channel width at spawning sites averaged 36.5 m (SD = 6.5 m, *n* = 30).

Almost half (49%) of the males but fewer females (17%) with transmitters moved below the dam after spending some time upriver (Table 3), as indicated in the 2003 season by a raft survey on 9 March and in 2004 by the listening station at the dam. The 23 fish that moved below the dam in 2004 spent 2.6 h to 37 days (mean = 12.3 days, SD = 9.7 days) in the ladder facility and area above the dam after tagging, and there was no relationship between downstream movement past the dam and Cedar River discharge or discharge change from the previous day (GLS, $p > 0.05$).

Total movement of radio-tagged coho salmon

Patterns of movement within the new habitat differed dramatically between the sexes, as illustrated by the detailed

Fig. 3. Daily counts of adult coho salmon (*Oncorhynchus kisutch*) moving upriver through the fish passage facility with Cedar River mean daily discharge for (*a*) 2003, (*b*) 2004, and (*c*) 2005 seasons. Note the different scales on the *y* axes.
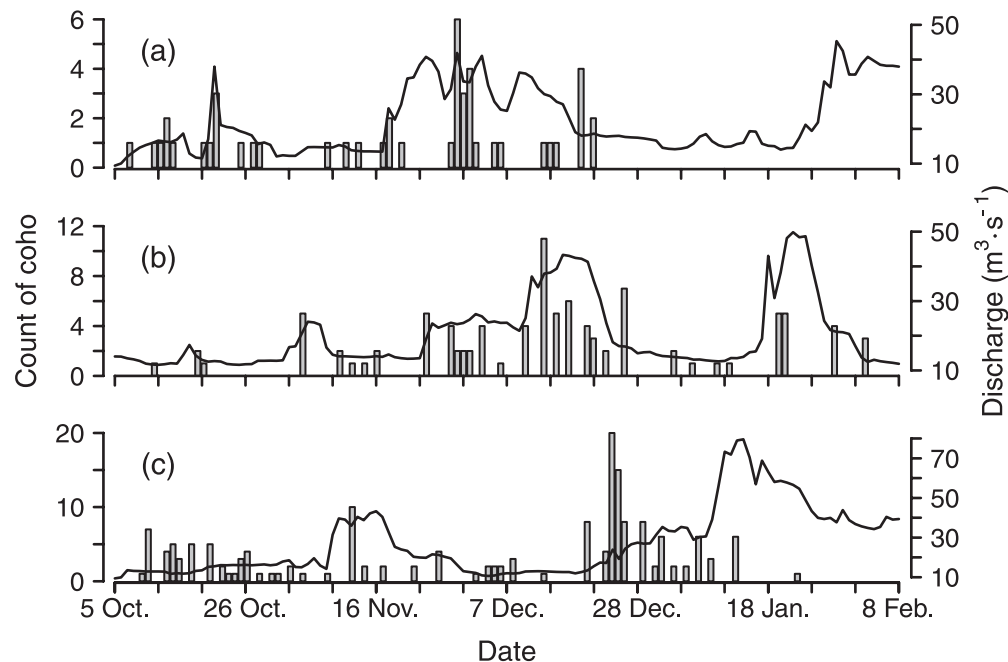

Table 1. Detection of radio-tagged coho salmon (*Oncorhynchus kisutch*) at listening stations, presented as the number of individual fish (*n*) and the proportion of all tagged salmon within that season.

Station	Distance (km)	*n* 2003	*n* 2004	Proportion (%) 2003	Proportion (%) 2004	Coverage (%) 2003	Coverage (%) 2004
Landsburg (LD)	0.0	—	49	—	100	—	100
Lower Rock (LR)	3.4	30	40	81	82	100	100
Middle mainstem (MM)	6.9	—	36	—	73	—	100
Taylor (TA)	12.5	5	10	14	20	97	100
Middle Rock (MR)	5.9	1	1	3	2	98	95
Upper Rock (UR)	8.0	0	0	0	0	81	50

Note: Distance refers to the longitudinal distance in river kilometres from the tag site at Landsburg Diversion Dam to the position of the listening station. Coverage represents the proportion of time during each season that the listening station was operational.

Table 2. Entrances by radio-tagged coho salmon (*Oncorhynchus kisutch*) into tributaries of the Cedar River.

	2003 Males	2003 Females	2004 Males	2004 Females
Number of individual salmon	12	3	17	1
Proportion of total tagged (%)	52	21	38	25
Number of total entrances	34	3	23	1
Mean entrances per individual	2.8	1.0	1.4	1.0
Proportion temporary (%)	97	67	100	100
Duration mean (h)	5.1	2.7	7.9	2.2
Duration standard deviation (h)	6.0	0.1	11.1	—
Duration maximum (h)	24.8	2.8	38.6	2.2

Note: With only two exceptions, these represent entrances into Rock Creek. The two exceptions occurred in 2003, when two different males each entered Taylor Creek once.
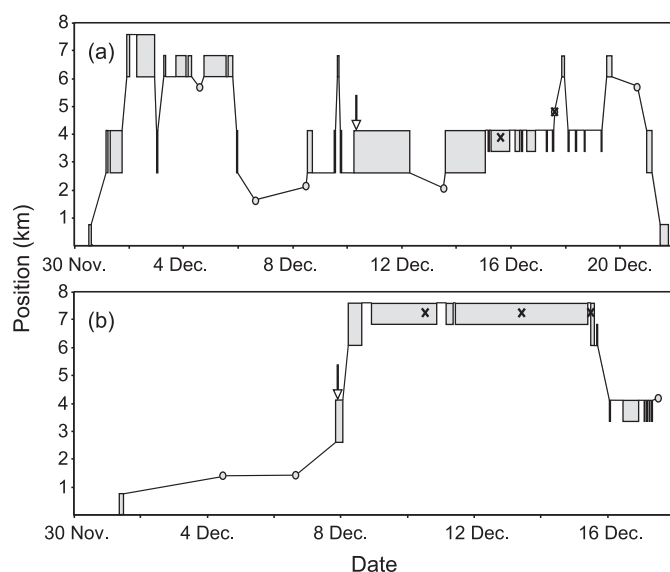
movement histories of one representative male and female (Fig. 4). The male's total distance moved (45.8 km) was very similar to that of the male population median in that season (45.0 km) even though he was never detected more than 7.6 km upriver from the dam. Instead, he moved frequently within that stretch of river until exiting below the

Table 3. Final locations of radio-tagged coho salmon (*Oncorhynchus kisutch*) with respect to Landsburg Diversion Dam.
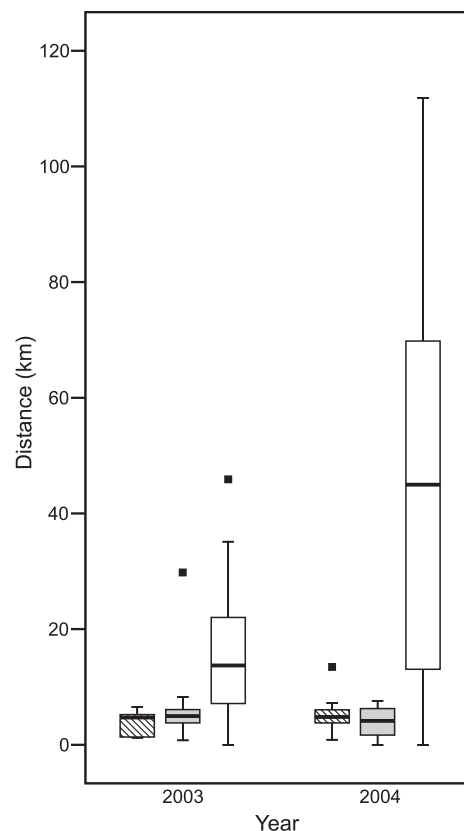
Sex	Year	Above dam	Below dam	Unknown
Males	2003	10	10	3
	2004	23	22	0
Females	2003	12	2	0
	2004	3	1	0

Fig. 4. Detailed movement history of typical (*a*) male and (*b*) female coho salmon (*Oncorhynchus kisutch*). Date and time are along the *x* axis, and longitudinal position within the Cedar River is on the *y* axis. The boxes are listening station detections, where the width is proportional to the duration and the height is proportional to the estimated detection range. Boxes of half height are detections where an individual remained exclusively above or below the station itself. Mobile detections are represented by circles. Arrows are temporary tributary entrances, and "×" denotes a direct visual observation of the animal on a redd. The male was observed on two different redds, whereas the female was observed on a single redd multiple times. Movement distance for the male was summed up to the final detection at the MM station on 19 December. This individual passed downriver past Landsburg Diversion Dam on 21 December. The female in the bottom panel was detected repeatedly in the same location as shown by the final mobile detection plotted on 17 December before the carcass was recovered at this same location on 7 January.


Fig. 5. Coho salmon (*Oncorhynchus kisutch*) spawning site distances and total movement of radio-tagged colonists within the newly accessible habitat. From left to right within each year are redd distances (hatched boxes, *n* = 5 in 2003, *n* = 18 in 2004), female movement (shaded boxes, *n* = 14 in 2003, *n* = 4 in 2004), and male movement (open boxes, *n* = 21 in 2003, *n* = 45 in 2004). In each plot, the thick middle bar is the median, the boxes represent the interquartile range, and the remainder of the data is contained in the whiskers and outliers points (solid squares). Redd distances are measured from Landsburg Diversion Dam in river kilometres. Comparing movement between seasons is not valid because of the addition of two listening stations and increased frequency of mobile telemetry surveys in 2004.

dam 21 days after entry. The female moved upriver more slowly, briefly explored Rock Creek, and established her redd site 7.2 km above the dam approximately 8 days after tagging. She never undertook the extensive back and forth movements characteristic of most males (total distance moved = 7.6 km; 2004 female population median = 4.1 km) and remained in the vicinity of her redd site until the final downriver movement that was assumed to be carcass drift 14 days after ascending the ladder. Males (average minimum estimate = 34.8 km, *n* = 66) moved much more than females (5.8 km, *n* = 18; Fig. 5). Estimates of minimum movement

were higher in 2004, primarily because the two additional telemetry stations increased our power to detect movement, but males moved more than females in both 2003 (Mann–Whitney *U* = 59.0, *p* = 0.003) and 2004 (Mann–Whitney *U* = 28.5, *p* = 0.03). Median total movement of females within the new habitat was approximately equal to the median of the upriver distance of identified redds (Fig. 5).

Female movement was not significantly related to migration date, body length, or Cedar River discharge (single predictor variable ordinary least squares regression, all *p* > 0.05). Similarly, male movement was unrelated to migration date, body length, and discharge (all *p* > 0.05). However, male movement was negatively related to the estimated number of ripe females within the new habitat (*p* = 0.008, r^2 = 0.10; Fig. 6); males moved more when females were scarce. To further explore the relationship between estimated count of ripe females and male movement, we compared linear and quadratic ($y = ax^2 + bx + c$) models. The quadratic model

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Fig. 6. Relationship between estimated number of receptive females and total movement by individual male coho salmon (*Oncorhynchus kisutch*) in 2003 (open circles, $n = 21$) and 2004 (solid circles, $n = 45$). Quadratic models of total movement are shown as a broken line for 2003 ($p = 0.04$, $r^2 = 0.29$) and a solid line for 2004 ($p = 0.004$, $r^2 = 0.31$). On the y axis, zero represents average movement within each year, and the values are the number of standard deviations away from the annual mean.
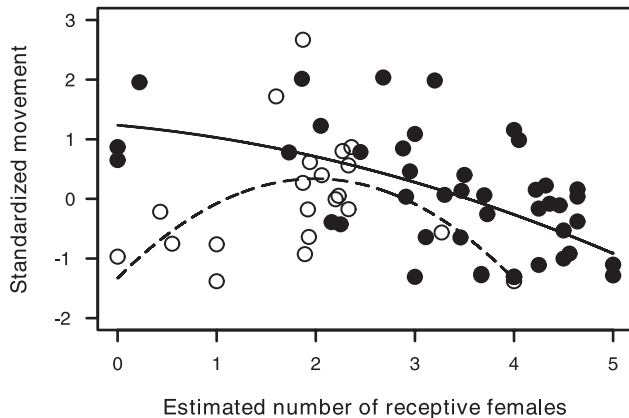
better fit the 2003 data ($n = 21$; linear, $p = 0.7$; quadratic, $p = 0.04$, $r^2 = 0.29$), but the models performed equally well for the 2004 data ($n = 45$; linear, $p < 0.0001$, $r^2 = 0.30$; quadratic, $p = 0.0004$, $r^2 = 0.31$). Tagged males had access to more ripe females in 2004 (average = 3.4) compared with 2003 (average = 1.9). The linear model performed well when there were >3 females (densities this high were rare in 2003 but more common in 2004) but poorly when females were scarce. The quadratic model performed well in 2003 because it captured a dome-shaped relationship (Fig. 6); male movement was greatest at intermediate levels of female availability. Thus there was strong evidence from both years that males seldom moved when females were numerous, and weak evidence from 2003 that male movement was also reduced when females were scarce (Fig. 6).

Discussion

Dam passage

The first objective was to document the basic ecological attributes of coho salmon entering newly accessible habitat. Colonization began in the very first season when Landsburg Diversion Dam was passable; 47 coho salmon moved upriver in fall 2003, increasing to 99 in 2004, and 170 in 2005. Obviously these original colonists did not return to their natal site, as the habitat extension afforded by the passage facilities permitted range expansion by salmon spawned in the Cedar River below the dam and straying from elsewhere. Although the origin of the colonists is unknown, it seems reasonable to assume that many, if not most, were produced in the 35 river kilometres of the Cedar River or its tributaries below the dam. Very few had clipped adipose fins indicating hatchery origin, and both hatcheries in the Lake Washington basin (University of Washington and Issaquah Creek) clipped at least 93% of their juvenile coho salmon in the appropriate release years (Regional Mark Processing Center database, www.rmpc.org). Thus the vast majority of colonists were

naturally spawned. The counts of coho salmon ascending the ladder increased in successive years, but the lack of comprehensive abundance data on coho salmon below the dam makes it impossible to determine whether this reflects higher rates of colonization or merely increases in coho salmon throughout the system.

Basic population demographics revealed three interesting observations. First, as a result of low abundances and protracted timing, instantaneous spawning densities were extremely low (average daily estimate of ripe females above dam = 1.8 in 2003, 1.8 in 2004, and 4.5 in 2005). Second, in all three seasons, more males entered the new habitat than females. This may reflect, in part, the generally higher survival of male coho salmon at sea and overabundance relative to females in many populations (Holtby and Healey 1990; Spidle et al. 1998). In addition, males may have been more likely to enter the fish passage facility because of their elevated movement rates compared with that of females. Third, we observed a large proportion of small males, presumably age-2 jacks, in 2005. The sudden abundance of this age class in 2005 after 2 years of absence raises the possibility that these fish were the offspring of the original 2003 brood year, homing to natal sites above the dam. However, the proportion of jacks within a population varies between years (Vøllestad et al. 2004), so the abundance of jacks in 2005 may have resulted from processes unrelated to homing such as smolt size or overall year-class strength.

Passage results were also used to evaluate the proximate environmental stimuli promoting upriver movement through the ladder. The idea that higher stream flows induce upriver movement by adult salmon has been discussed for decades (Davidson et al. 1943; Shapovalov and Taft 1954; Banks 1969), though fish may respond to changes in flow rather than the absolute value (Trépanier et al. 1996). In two years, both absolute discharge and change from the previous day were positively related to ladder counts, but no discharge effect was observed in 2005, likely because many of the high flow days occurred toward the end of the season when few fish were left to enter. Similarly, Erkinaro et al. (1999) noted that point-checking data, such as the ladder counts used in this study, will tend to underestimate the effects of environmental stimuli if there are no fish available downstream of the counting location. In contrast to discharge, temperature showed no clear effect on passage.

Spawning sites

The second objective was to assess reach-scale patterns in spawning site selection and evaluate the hypothesis that coho colonists would spawn primarily in tributaries. Coho salmon spawn in small streams elsewhere in the Lake Washington basin and in tributaries of the Cedar River below the dam, and this species is typically found in small streams of intermediate gradient (Sandercock 1991), so we expected extensive use of Rock Creek for spawning. We cannot rule out the possibility that untagged coho salmon spawned in tributaries but we found no evidence of tagged fish spawning in tributaries despite continuous monitoring of Rock Creek and Taylor Creek via telemetry listening stations and periodic mobile tracking surveys of all four tributaries. Listening station data showed that 38% of tagged salmon entered Rock

Creek for temporary visits, but these trips were of insufficient duration for spawning. These temporary entrances indicated that the lack of tributary spawning was not because salmon were unable to locate tributaries; these areas were simply not selected. Furthermore, snorkel surveys indicated that juvenile coho salmon were absent from Rock Creek for much of the spring and early summer but apparently entered from the mainstem later in the growing season (Anderson 2006). Unfortunately, the lack of information on the relative frequency of tributary versus mainstem spawning below the dam prevents quantitative comparisons to breeding habitat preferences elsewhere in the watershed.

There are at least two possible explanations for why coho salmon did not spawn in the tributaries, as seems to be typical for the species (Sandercock 1991). First, the Cedar River may represent higher-quality adult spawning habitat and mainstem redd locations resulted from behavioral choice. The temporary exploration of Rock Creek by 38% of tagged salmon in both telemetry seasons is consistent with this hypothesis, as fish accessed the tributary habitat but did not spawn there. The second possibility is that coho salmon colonists did not imprint on the odors of the tributaries and thus were more reluctant to settle there. Under this scenario, the Cedar River below the dam was the source of colonists. Within the range of odors presented by the new habitat, Cedar River odors were more similar to those of natal sites below the dam than those of the tributaries, especially if the fish had been spawned in the Cedar River itself rather than in the tributaries below the dam. For example, the concentration of total organic carbon in Rock Creek (mean ± 1 SD = 2.9 ± 1.4 mg·L^{-1}) was more than four times greater than in the Cedar River (measured just upriver from the Rock Creek confluence: 0.7 ± 0.2 mg·L^{-1}; P. Kiffney, National Marine Fisheries Service, 2725 Montlake Blvd East, Seattle, WA 98112, USA, unpublished data). Perhaps the colonists identified differences in organic carbon or other chemical signals and chose spawning locations based on olfaction despite the absence of authentic homing cues, overcoming a general attraction to tributaries for breeding.

Movements of individual salmon

Our third objective was to quantify individual movement within the new habitat and evaluate the prediction that movement would be inversely correlated with breeding opportunities. Movements of radio-tagged salmon were highly variable, as some individuals moved over 100 km within the habitat, whereas others spent only hours above the dam before returning downstream. The most striking pattern was that males moved significantly more than females. Sex-based movement differences have been previously observed (McCubbing et al. 1998; Hutchings and Gerber 2002) and likely can be explained by differing sources of breeding competition. Female salmon compete with each other for access to spawning territories (Schroder 1981; van den Berghe and Gross 1989; Foote 1990). Densities of female salmon in our study were very low and potential spawning sites were abundant, so females had little need for widespread movement. Males, on the other hand, compete with each other for access to ripe females (Schroder 1981; Foote 1990; Quinn et al. 1996). With few potential mates, far-ranging movement

may have been needed to find a receptive female. Competitively inferior males may have been displaced from available mates, and then moved to find a female, perhaps unsuccessfully, for which they could compete (Healey and Prince 1998). Furthermore, males often depart females in search of other breeding opportunities immediately after a spawning event, whereas females remain to guard the nest site (Foote 1990). Males moved more when receptive females were scarce, further supporting the prediction that breeding opportunity and movement would be inversely related. There appeared to be a threshold effect, whereby male movement was extremely variable and unrelated to female availability until there were at least three females to court. Beyond this threshold, female abundance had a clear inverse relationship with male movement.

The total movement values we report for male colonists vastly exceed those of other studies recording salmon movement on the spawning grounds, and we propose two potential explanations. First, the colonists in this study may have been a nonrandom subset of the source population, predisposed to extensive movements because they were competitively inferior. Healey and Prince (1998) observed that satellite males moved more widely than alpha males. Perhaps the colonists in the present study entered the new habitat because they were excluded from breeding opportunities below the dam. Second, observed spawning densities in the Cedar River were much lower than in previous movement studies of >1000 fish·km^{-1} for stream-spawning sockeye (Stewart et al. 2004; Rich et al. 2006), >0.5 fish·m^{-2} for beach-spawning sockeye (Hendry et al. (1995), and approximately 150 fish·km^{-1} for coho spawning in a small creek (Healey and Prince 1998). We observed an effect of density, and male movement might have been further reduced at even higher female densities.

Adult salmon movements can be divided into different phases: (*i*) migratory, a period of comparatively rapid upriver movement, (*ii*) search, a phase of erratic upriver and downriver movements (Økland et al. 2001; Connor and Garcia 2006), and (*iii*) spawning movements. The movements observed here exceeded those previously reported for spawning behavior, but they were quite similar to those reported for search behavior. Migrating salmon move much more rapidly (10–50 km·day^{-1}; Keefer et al. 2004) than fish on spawning grounds (0–1 km·day^{-1}; Healey and Prince 1998). Many of the far-ranging movements by males reported here (average minimum estimate = 34.8 km) were repeated upriver and downriver excursions and were similar to search distances previously reported for Chinook (wild male average = 39 km; Connor and Garcia 2006) and Atlantic salmon (*Salmo salar*; both sexes, 1992 average = 30.9 km, 1993 average = 22.8 km; Økland et al. 2001).

Body size, entry date, and discharge were not significantly correlated to the total movement of individual fish, although many salmon were present during periods of increased discharge, particularly in 2004. Consequently, males may have moved less at higher flows because more females were available to court. However, movement into tributaries was positively related to Cedar River discharge in both telemetry seasons. This movement was predominantly temporary, and fish may have been escaping high flows encountered in the

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mainstem, exploring potential breeding habitat, or searching for mates. Thus the results for discharge were mixed; salmon moved upriver through the ladder and into tributaries during periods of increased flow but discharge was not related to the total movements of radio-tagged individuals. Discharge likely provided a stimulus for upriver movement before fish reached sexual maturity. Once reproductive behavior dominated movements, discharge was no longer an important factor, consistent with the idea that discharge and sexual maturity interact to affect adult salmon movement (Davidson et al. 1943).

In both seasons, roughly half of the tagged males, and a lower proportion of tagged females, moved below Landsburg Diversion Dam after spending some time upriver. It is unlikely that this is purely the result of carcass drift, as carcasses tended to settle in a large, deep pool immediately upriver from the dam. Moreover, if downstream movement was the result of carcass drift, it would have been positively related to discharge and occurred in equal proportions for both sexes, but neither result was observed. The frequency of downstream passage by males was likely related to their higher overall movement rate, as they may have moved downriver in search of mates. Many Chinook salmon passing downriver over Columbia River dams later entered spawning grounds or hatcheries, suggesting that salmon may retreat if they "overshoot" their natal site (Boggs et al. 2004). Interestingly, the lone radio-tagged female in 2004 that moved below the dam spent approximately 6 h above the dam before retreating downriver and was observed on a redd, courted by two males 3.1 km below Landsburg Dam, 5 days after tagging.

Colonization, homing, and conservation

In this initial phase of population expansion, all colonists were strays; they could not be homing precisely to their natal site because this area had not been accessible for the last 100 years. Salmon accessing the new habitat either failed to home accurately or strayed by choice. Salmon use olfactory cues to identify their natal site (Dittman and Quinn 1996). A failure to home could have occurred if there were no odor differences between the Cedar River above and below the dam, or if fish could not detect the differences. Previous studies have demonstrated that salmon are capable of detecting differences in olfactory cues at the reach scale within a single creek or river (Wagner 1969; Stewart et al. 2004; Quinn et al. 2006). Local geology will likely have a strong influence on site-specific odors, and thus the spatial scale at which detectable differences occur will vary substantially between watersheds. Alternatively, the odors of conspecifics could have played a role in the colonization process. In each successive year of coho salmon passage, increased adult counts followed increased densities of juvenile coho salmon observed the previous summer (Anderson 2006). This observation is consistent with the pheromone hypothesis advanced by Nordeng (1971; 1977), as adult colonists may have received an olfactory cue from the previous year's offspring. Experimental studies indicated that adult coho salmon were attracted to the odors of juvenile coho salmon (Quinn et al. 1983), but it is unclear to what extent these odors affected movements in the Cedar River. It is also possible that

changes in coho salmon abundance within the entire system caused the increasing numbers of colonists.

In addition to the physiological explanations, salmon may have strayed into the new habitat by choice. Female salmon colonists had virtually no competition for breeding space (e.g., van den Berghe and Gross 1989), so they could devote their energy almost entirely to nest site selection and preparation rather than territory acquisition and defense. In addition, they encountered a biologically and physically well-developed stream community, with abundant pools, instream woody debris, and prey base for offspring. This high-quality habitat contrasts with the young streams made available by retreating glaciers (Milner and Bailey 1989; Milner et al. 2000), and it would be interesting to compare movements of salmon in these systems. There likely exists a trade-off between precise homing and spawning habitat selection whereby salmon establish nests away from their natal site if local conditions elsewhere are better (Stewart et al. 2004). In this case, female colonists may have detected differences from odors imprinted elsewhere, but settled above the dam because of the low competition and high habitat quality.

In conclusion, we have documented the initial process of population expansion whereby adult salmon colonized an area from which they had been extirpated for over 100 years. The number of salmon that entered the new habitat via the dam passage facility, as well as the widespread movements of some salmon above the dam, suggests that exploration is an innate component of salmon breeding behavior. The more restricted movements of females compared with males, in addition to their smaller numbers of gametes, suggests that female dispersal will likely limit the numerical and spatial expansion of the population in the first few generations. Clearly, dispersal ability benefits salmon when new habitat becomes available, but Pacific salmon also possess other traits identified by Safriel and Ritte (1983) as common to good colonizers, including rapid growth, early reproductive maturity, and large reproductive effort (Quinn 2005). The establishment of a self-sustaining population following colonization will also depend on the reproductive success of salmon after arriving in the new habitat. Thus, in the Cedar River, the survival of offspring rearing in a community of competitive and predatory resident fish will likely determine the population's future trajectory.

The ability to exploit new habitat implies that dam circumvention projects have great potential to benefit salmon populations. Freshwater habitat loss threatens salmon throughout much of their range, and dams have dramatically reduced access to spawning and rearing areas (Nehlsen et al. 1991). Agencies tasked with aiding the recovery of salmon may take a variety of approaches. Although artificial supplementation offers one option to seed unoccupied habitats (Young 1999), genetic risks of translocation may outweigh potential benefits (Utter 2001; Eldridge and Naish 2007). Alternatively, stream restoration can recuperate natural fluvial and biological processes in lotic ecosystems to the benefit of salmon. Despite substantial funding for such projects, limited evaluation of outcomes has restricted our ability to learn from mistakes and achievements (Bernhardt et al. 2005). In planning stream restoration activities, management should prioritize reconnection of isolated high-quality habitats (Roni et al. 2002). Our results demonstrate that salmon

are apt to disperse into new areas, and continued documentation of natural recolonization rates and processes will help managers identify migration barriers suitable for removal or circumvention. Restoring access to lost habitats will provide opportunities for salmon to explore, colonize, and recover.

Acknowledgements

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