Dispersal and tributary immigration by juvenile coho salmon contribute to spatial expansion during colonisation

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Abstract – Anadromous fishes are frequently restricted by artificial barriers to movement such as dams and culverts, so measuring dispersal helps identify sites where improved connectivity could promote range expansion and population viability. We used a combination of DNA-based parentage analysis and mark–recapture techniques to evaluate dispersal by juvenile coho salmon (Oncorhynchus kisutch) in a population in the initial stages of colonisation following installation of fish passage structures at a previously impassable dam on the Cedar River, WA, USA. The spatial distribution of individuals within maternal families revealed that dispersal was common. Among the offspring of radio-tagged mothers, 28% were collected outside the spawning reach and dispersed up to 6.3 km (median = 1.5 km). Most juveniles captured in a tributary (Rock Creek, where few adults spawned) had immigrated from the Cedar River and represented many different families. Juvenile dispersal therefore provided a secondary phase of spatial expansion following initial colonisation by adults. Consistent with the condition-dependent dispersal hypothesis, juveniles that dispersed farther upstream in the tributary were larger than fish collected near the tributary mouth. Overall, the results demonstrated widespread dispersal in a system with low coho salmon densities, and this might increase the rate of population growth if it reduces the effects of local density dependence. By implication, juveniles can take advantage of rearing habitats reconnected through barrier removal, even when such areas are located several kilometres from adult breeding grounds.

Key words: movement; condition dependence; reintroduction; parentage; pedigree; dams

Introduction

Dams and other artificial barriers to movement reduce the connectivity of river networks, posing a serious threat to many species of migratory freshwater fish (Morita & Yamamoto 2002; Limburg & Waldman 2009). For anadromous Pacific salmon (Oncorhynchus spp.), impassable barriers eliminate habitat and are a primary cause for declining runs in Washington, Oregon, Idaho and California (National Research Council 1996). However, there is a growing appreciation that barrier removal or circumvention provides unique opportunities for salmon conservation (e.g., Pess et al. 2008).

Dispersal permits the colonisation of new habitat, so its measurement is critical to conservation efforts that identify sites where improved connectivity could promote range expansion of anadromous species. Some adult salmon ‘stray’ into non-natal streams for reproduction (Hendry et al. 2004), and this is the primary mechanism for colonisation (Anderson & Quinn 2007; Pess et al. 2012). However, juvenile
salmon may move substantial distances within streams (Ebersole et al. 2006), so juvenile dispersal may produce a secondary phase of spatial expansion following initial colonisation by adults. Moreover, if juveniles disperse within streams, maintaining connectivity to high-quality rearing habitats will benefit salmon populations even if these areas are rarely used for reproduction and are distant from spawning grounds.

Juvenile salmonids are ideal organisms for the study of dispersal because some level of dispersal is required based on the breeding ecology of adults and density-dependent foraging ecology of their juvenile offspring. Female salmonids deposit hundreds to thousands of eggs (depending on the species) in discrete nest sites (Esteve 2005); thus, juveniles emerging from a single nest site (termed ‘redd’) are initially aggregated. In most cases, the female constructs a single redd (Murdoch et al. 2009), so all maternal half-siblings emerge in the same vicinity. Juvenile salmon of stream-rearing species establish foraging hierarchies in which dominant individuals acquire and defend the most profitable territories (Fausch 1984). When space for such territories is limited, individuals move from high-density sites and this dispersal ultimately reduces the effects of density-dependent mortality (Keeley 2000; Einum et al. 2006).

Furthermore, rivers and streams are highly variable, spatially and temporally, in habitat attributes affecting fish growth and survival. Thus, dispersal between patches of varying quality may influence the fitness of individuals, thereby favouring the evolution of this behaviour. Movements of juvenile coho salmon (*O. kisutch*) are strongly seasonal as fish in coastal regions seek refuge in off-channel alcoves and ponds or tributaries of larger rivers in late fall or winter as river discharge increases (Peterson 1982; Nickelson et al. 1992; Bramblett et al. 2002). Occupancy of such tributaries may increase winter survival, relative to fish in the main river (Ebersole et al. 2006).

Two hypotheses make contradictory predictions regarding the relationship between individual propensity for dispersal and body size. The conventional view, commonly called competitive exclusion, is that space in streams is often limiting and dominance relationships are size-biased. Thus, smaller fish, which are presumably subordinate and unable to acquire territories, are more prone to disperse (Chapman 1962; Nielsen 1992; Webb et al. 2001). An alternative perspective is that dispersal is condition dependent, so larger individuals with greater energy reserves can move farther (Bowler & Benton 2005). The pattern of density-dependent dispersal at older but not younger life stages observed by Einum et al. (2006) supports this hypothesis. The distinction between these perspectives, which need not be entirely mutually exclusive, is especially important in a conservation context because they may determine patterns of dispersal during colonisation periods.

In this study, we describe the dispersal of stream-rearing juvenile coho salmon during the initial stages of colonisation following modification of Landsburg Diversion Dam on the Cedar River, WA. Almost all spawning took place in the Cedar River itself, but observations of juvenile coho salmon in Rock Creek, a tributary, provided indirect evidence for dispersal (Anderson et al. 2008). Here, we extend these results using DNA-based parentage to evaluate the spatial arrangement of maternal siblings (i.e., fish sharing a mother) because these individuals emerged from the same nest site. For some families, we had additional information on the location of the nest from a tag implanted in the mother. We sought to unequivocally determine whether individual juveniles sampled in the tributary had immigrated there and the extent to which the tributary habitat was used by juveniles from different families. To evaluate the competitive exclusion and condition-dependent hypotheses, we compared the body size of juvenile coho salmon expressing different dispersal behaviours. Based on the previous observation that juveniles collected farther upstream in Rock Creek were larger (Anderson et al. 2008; Pess et al. 2011), we hypothesised that condition dependence would govern upstream dispersal in the tributary.

**Materials and methods**

**Study site description**

The Cedar River is a 487-km² watershed in Western Washington, draining westward from the crest of the Cascade Mountains into Lake Washington, which is connected to Puget Sound via a man-made shipping canal. Landsburg Diversion Dam, a low-head, run-of-the-river dam, blocked migration of anadromous fish from 1901 until construction of fish passage facilities in fall 2003 made available 33 km of habitat in the Cedar River and its tributaries. Approximately 20 km of habitat is now accessible to salmon in the Cedar River itself between the dam and Cedar Falls, a natural barrier to migration, and 13 km is now accessible in tributaries, primarily Rock Creek, which enters the Cedar River 3.4 km upstream from the dam (Fig. 1). The City of Seattle now manages the area above the dam for municipal water supply and as a de facto reserve, without development, recreation or commercial logging. Further details on the habitat and biological community are given by Kiffney et al. (2009).
Sampling

Adult coho salmon were sampled as they bypassed the dam; species and sex were recorded, and a small piece of fin tissue was removed for subsequent DNA analysis. Some of the adults in 2003 and 2004 were given radio tags, and their movements were recorded using stationary and mobile tracking (details in Anderson & Quinn 2007). Although precise breeding locations could not be determined, we were able to assign some tagged females to ~1-km spawning reaches based on their movement patterns. No adults in 2005 received any kind of tag. In 2006 and 2007, we implanted passive integrated transponder (PIT) tags (wrapped in sponges to prevent regurgitation) via oesophageal implant into adult salmon. Adults were detected if they entered Rock Creek by an array of three channel-spanning antennas positioned at the mouth of the tributary designed to assess the directionality of movements (further details in Pess et al. 2011). For the fall–winter period when adults were breeding during these two seasons, at least one antenna (95.4% of the time) and often two antennas (85% of the time) were properly functioning. Our system was capable of detection efficiencies approaching 100% (Pess et al. 2011), consistent with similar systems operated by others in small streams (Connelly et al. 2008). Temperature loggers, placed within pools in the Cedar River and Rock Creek, recorded data hourly.

In this region, juvenile coho salmon typically rear in fresh water for one year following emergence from the spawning nest prior to seaward migration (Weitkamp et al. 1995). Juvenile coho salmon from brood years (BY: year in which their parents spawned) 2003 and 2004 were collected from sites throughout the Cedar River (Table 1). We sampled by seine net during the summer and covered the range of locations used by adults for spawning the previous fall (Anderson et al. 2008). Distinct shoals were sampled such that all individuals collected from a given site were captured in a relatively small area (approximately 10 m²). Locations were recorded with a handheld GPS device, and fin clips for subsequent DNA analysis were collected from all fish.

We used electrofishing to estimate density (fish m⁻²) and collect tissue samples from coho salmon in Rock Creek. Sampling for BY 2003 was limited to the lower 500 m of Rock Creek, but from BY 2004 onwards, we expanded the surveys to include approximately 50 distinct pools in three reaches (reach 1: 0.0–0.5 km from mouth of Rock Creek; reach 2: 1.7–1.9 km; and reach 3: 2.3–2.6 km). We sampled in summer (July or August) and fall (late September or October), approximately two months apart within each year. Fin clips for BY 2003 and 2004 fish were taken during the summer, fall and an additional winter sampling event (Feb or March), but fin clips for BY 2005–2007 fish were only taken during the fall sampling period (Table 1). For BY 2005 and 2006, we captured some juvenile coho salmon in the Cedar River and implanted PIT tags in fish >55 mm (but did not take genetic samples) to assess movement into Rock Creek.
Analysis

Coho salmon were genotyped using protocols previously described by Anderson et al. (2010). Adults \( N = 644 \) and juveniles \( N = 1719 \) with \( \geq 7 \) loci genotyped were included in this analysis, but the vast majority (88.3%) were genotyped at \( \geq 9 \) loci. Genotyping error rate was assessed at 0.66% (Anderson et al. 2010). We used Cervus version 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007) for all parentage analysis. All juvenile offspring were of known age, and we therefore only considered parents from the correct cohort. Subsequent assignment protocols were identical to those detailed in Anderson et al. (2010). Juveniles were assigned two parents if a potential parent pair met four criteria: (i) log of the odds score (LOD) \( \geq 12.44 \), (ii) \( \leq 1 \) mismatching locus, (iii) parents of the opposite sex and (iv) fewer mismatching loci than any other parent pair meeting criteria i–iv. Juveniles not assigned two parents were assigned a single parent if the candidate parent had (i) LOD \( \geq 6.21 \), (ii) \( \leq 1 \) mismatching locus and (iii) fewer mismatching loci than all other potential parents. LOD thresholds for both two- and one-parent assignments were obtained by simulation at the 99% confidence level. Across all brood years, we obtained genotypes from 1719 juveniles, and 1442 (83.9%) of them were assigned two parents. An additional 105 (6.1%) juveniles were assigned a mother only and so were suitable for analysis of dispersal.

Our analysis of dispersal focused on juvenile coho salmon that shared a mother, and we assumed these individuals emerged from a common redd. The redd typically consists of a series of 4–5 egg pockets, deposited discretely over a period of a few days and often fertilised by different males, but all guarded by the mother until she dies (Esteve 2005). We term these groups ‘maternal families’, because they contain both full- and maternal half-siblings.

To evaluate the condition dependence and competitive exclusion hypotheses, we compared the body size of juveniles that differed in dispersal behaviour. We had previously found that the offspring of later-spawning females were smaller (Anderson et al. 2010) and therefore accounted for this effect in our analyses. For BY 2003 and 2004, we compared the body size of dispersing and nondispersing juveniles within families because these individuals shared a common emergence date. This analysis was restricted to samples collected during the summer from families with at least three juveniles in both the dispersing and nondispersing categories. For BY 2006 and 2007, we compared the body size of immigrants that dispersed from the Cedar River into the upper reaches of Rock Creek with those that dispersed from the Cedar River into the lower reach of Rock Creek. ANCOVA simultaneously tested the effects of date of maternal arrival to the spawning grounds (continuous) and upstream versus downstream capture location (categorical). ANCOVA, performed separately for each brood year, first tested a full model with the interaction term; the interaction term was subsequently dropped if it was nonsignificant \( (P > 0.10) \).

Results

Within each cohort, a large proportion of the total number of females that bypassed the dam produced offspring in our collections (Table 1). Samples of juvenile coho salmon from BY 2003 and 2004, when both the Cedar River and Rock Creek were sampled, indicated extensive dispersal. We considered the spatial distribution of 27 maternal families with \( \geq 12 \) individuals (Figs 2 and 3). For eight families, the
spawning reach was known from radio-tracked movements of the mother assigned via parentage analysis. Of the 220 juvenile coho salmon in these families, 62 (28%) were collected outside the spawning reach and had moved as much as 6.3 km (median = 1.5 km) from the spawning reach (Fig. 4). For some of the families without maternal radio-tracking data, a pronounced peak in juvenile abundance indicated a likely breeding location (Figs 2h–j and 3b–l). However, most of these families (12 of 14) also had at least one individual collected >1 km from the presumed spawning reach (Figs 2h–j and 3b–l). Although the predominant direction of movement in the Cedar River was downstream, many families with known or inferred spawning reaches had individuals that moved upstream, particularly in BY 2004.

Fig. 2. Spatial histograms of maternal families from brood year 2003. Each panel a–j represents a single family. The large histogram shows samples taken from the Cedar River, and the small inset plot shows samples taken from Rock Creek, which enters the Cedar River 3.4 km from the dam. All Cedar River samples were collected during the summer (on or before September 15); Rock Creek samples taken during the summer are shown in black, whereas those taken in fall or winter are shown in grey. Spawning locations for families determined from radio tracking are denoted by the horizontal black bars. All tick marks for both the primary and inset plots are spaced at one-km intervals. Sampling within Rock Creek was limited to the lower 500 m.
Fig. 3. Spatial histograms of maternal families from brood year 2004. Each panel a-q represents a single family. The large histogram shows samples taken from the Cedar River, and the small inset plot shows samples taken from Rock Creek, which enters the Cedar River 3.4 km from the dam. All Cedar River samples were collected during the summer (on or before September 15); Rock Creek samples taken during the summer are shown in black, whereas those taken in fall or winter are shown in grey. The black bar denotes a spawning reach known from radio tracking; grey bars indicate spawning reaches inferred from family spatial distribution used in the comparison of body size between dispersers and nondispersers. All tick marks for both the primary and inset plots are spaced at 1-km intervals.
was also observed for juveniles that presumably emerged from nest sites in the Cedar River several kilometres above (Figs 2a,b,d, and 3a,h,i) and below (Fig. 3c,l) the tributary junction.

Beginning with BY 2004, we sampled multiple reaches in Rock Creek. Densities increased from summer to fall in almost all reaches and all years, the only exception being reach 1 in BY 2005 (Table 2). Densities in the upstream reaches increased more from summer to fall than the lowest reach (Table 2). Parentage analysis indicated that juvenile coho salmon collected from Rock Creek represented many different maternal sibling families (Table 1). The proportion of females bypassing the dam that produced juvenile offspring collected from Rock Creek increased in each successive year (Table 1). Juvenile coho salmon collected from the upstream reaches in Rock Creek tended to be produced by adult females that bypassed the dam earlier than the mothers of the juveniles collected from the lower reach (Table 2), a difference that was statistically significant in three of four cohorts ($t$-tests for reach 1 versus reaches 2 and 3 pooled: BY 2004: $P = 0.038$, BY 2005: $P < 0.0001$, BY 2006: $P = 0.016$, BY 2007: $P > 0.10$).

To evaluate patterns of tributary immigration by juvenile coho salmon from BY 2006 and 2007, we examined the PIT-tag detection histories of the adult females that produced these cohorts. Consistent with results from previous years (Anderson & Quinn 2007; Anderson et al. 2008), most females spawned in the Cedar River and few entered Rock Creek. We tagged 70 (88%) of the females in 2006, and only 10 of them were detected in Rock Creek. Of those 10 females, four exited the creek <24 h after entering and therefore almost certainly did not spawn there. Of the remaining six fish, three appeared to spawn in

![Fig. 4. Distance from collection site to spawning reach for 62 juvenile coho salmon that dispersed from known breeding locations. White bars are Cedar River (summer, on or before September 15), black bars are Rock Creek (summer), and grey bars are Rock Creek (fall and winter). All individuals are from families 2a–g in Fig. 2 and 3a in Fig. 3. Negative values indicate downstream movements from the nest site; fish sampled from Rock Creek include some upstream movement in the tributary but are expressed as a total distance from the nest site to the collection site. Values should be regarded as minimum but not precise estimates of dispersal distance because of uncertainty over the exact location of nest sites within spawning reaches.](image)

Table 2. Densities of juvenile coho salmon (fish·m$^{-2}$) within pools in three distinct reaches of Rock Creek.

<table>
<thead>
<tr>
<th>Brood Year</th>
<th>Reach</th>
<th>Summer density</th>
<th>Fall density</th>
<th>Maternal arrival date$^\dagger$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sites</td>
<td>Mean ± SD</td>
<td>Sites</td>
<td>Density $t$-test $P$-value</td>
</tr>
<tr>
<td>2004</td>
<td>1</td>
<td>0.0563 ± 0.0753</td>
<td>23</td>
<td>0.0382 ± 0.148 ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.0358 ± 0.0550 ns</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.0 ± 0.0</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td>2005</td>
<td>1</td>
<td>0.171 ± 0.181</td>
<td>23</td>
<td>0.148 ± 0.149 ns</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.0156 ± 0.0321</td>
<td>18</td>
<td>0.123 ± 0.206 0.044</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.0085 ± 0.0149</td>
<td>11</td>
<td>0.0718 ± 0.0510 0.0048</td>
</tr>
<tr>
<td>2006</td>
<td>1</td>
<td>0.131 ± 0.231</td>
<td>17</td>
<td>0.380 ± 0.478 0.065</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.0519 ± 0.0851</td>
<td>13</td>
<td>0.173 ± 0.181 0.043</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.150 ± 0.118</td>
<td>9</td>
<td>0.347 ± 0.201 0.022</td>
</tr>
<tr>
<td>2007</td>
<td>1</td>
<td>0.202 ± 0.328</td>
<td>18</td>
<td>0.204 ± 0.172 ns</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>–</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.0609 ± 0.130</td>
<td>11</td>
<td>0.522 ± 0.697 0.055</td>
</tr>
</tbody>
</table>

$^\dagger$Restricted to fall sample only.
Reach 1 is located 0.0–0.5 km from the mouth of the creek, and reaches 2 (1.7–1.9 km) and 3 (2.3–2.6 km) are further upstream. Welch’s $t$-test was used to compare densities between seasons within each reach year (ns indicates $P > 0.10$).
the creek and the other three had detections with ambiguous directionality of movement, making it difficult to determine whether they spawned in Rock Creek or exited prior to breeding. In 2007, we tagged 39 (74%) of the females, and none of them was detected in Rock Creek. This result was not attributable to equipment failure, as 16 of 65 tagged adult males were detected in Rock Creek during this season. After linking individual juveniles to maternal spawning behaviour via parentage, it was clear that the majority of juveniles sampled in Rock Creek had immigrated into the tributary from nest sites in the Cedar River (Table 3).

We also PIT-tagged juvenile coho salmon in the Cedar River and monitored their entrance into Rock Creek for BY 2005 and 2006. Overall, 20 of 338 (5.9%) of the juveniles tagged in the river entered Rock Creek, including a few individuals that moved upstream over 2 km in the Cedar River to the mouth of the tributary (Table 4). For BY 2006, when fish were tagged on multiple days and at multiple locations, there was no effect of tagging date on the likelihood of entering Rock Creek (generalised linear model with binomial errors, \( P > 10 \)), but there was an effect of tagging location (analysis of deviance from binomial GLM, \( P = 0.0015 \)); individuals marked and released 6.7 km above Rock Creek were more likely to enter the stream than those tagged 2.2 km below or 9.3 km above the tributary.

To evaluate the condition-dependent hypothesis, we compared body size in juveniles differing in movement patterns. Four families from BY 2003 (Fig. 2a–d) and ten families from BY 2004 (Fig. 3a–j) had at least three juveniles sampled within and three juveniles sampled outside a known or inferred spawning reach during the summer. Two-way ANOVA, performed separately on each cohort, found no difference in body size between juveniles found near the nest and those that dispersed away from it (BY 2003: \( F_{1,111} = 0.080, P = 0.78 \); BY 2004: \( F_{1,284} = 0.15, P = 0.70 \)), but there was a family effect (BY 2003: \( F_{3,111} = 24.8, P < 0.0001 \); BY

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Table 3. Juvenile coho salmon captured in Rock Creek, categorised according to the detection histories of adult females assigned to each individual juvenile via parentage analysis.

<table>
<thead>
<tr>
<th>Brood year</th>
<th>Sample</th>
<th>N</th>
<th>Not detected</th>
<th>Maternal Rock Creek detections</th>
<th>Visit†</th>
<th>Spawn‡</th>
<th>Uncertain§</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>Maternal families</td>
<td>42</td>
<td>36</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>Individual juveniles</td>
<td>186</td>
<td>108</td>
<td>2</td>
<td>64</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td>Maternal families</td>
<td>34</td>
<td>34</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td>Individual juveniles</td>
<td>191</td>
<td>191</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

†Exited Rock Creek <24 h after entering.
‡Upstream movement into Rock Creek without subsequent detections.
§Detected, but directionality ambiguous.

Table 4. Immigration into Rock Creek by juvenile coho salmon tagged in the Cedar River.

<table>
<thead>
<tr>
<th>Brood year</th>
<th>Tag location (km)</th>
<th>Tag date</th>
<th>Number tagged</th>
<th>Rock Creek immigrants</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>–0.2</td>
<td>Jul 12</td>
<td>47</td>
<td>9</td>
</tr>
<tr>
<td>2006</td>
<td>–2.2</td>
<td>Jun 20</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jul 17</td>
<td>115</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug 20</td>
<td>62</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>+6.7</td>
<td>Jun 21</td>
<td>21</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jul 18</td>
<td>27</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>+9.3</td>
<td>Jul 19</td>
<td>39</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug 30</td>
<td>18</td>
<td>1</td>
</tr>
</tbody>
</table>

Tag locations in the Cedar River are longitudinal distance in stream kilometres from the mouth of Rock Creek to the tagging site, where negative values indicate locations downstream from Rock Creek.

Fig. 5. Body size of immigrant juvenile coho salmon collected from the lower (open circles, 0.0–0.5 km from creek mouth) and upper reaches (filled circles, 1.7–2.6 km) of Rock Creek during fall surveys. All plotted individuals were assigned to adult females that received PIT tags and did not spawn in Rock Creek. The lines (solid = upper reaches, dashed = lower reach) denote predictions from an ANCOVA (body size ~ maternal arrival date + capture location).
2004: $F_{9,284} = 26.0, P < 0.0001$; the family × location interaction term was significant in BY 2004 ($F_{9,284} = 2.16, P = 0.025$) but not in BY 2003 ($F_{3,111} = 2.05, P = 0.11$).

BY 2006 and 2007 provided support for condition-dependent upstream dispersal within Rock Creek. For juvenile salmon known to originate from nest sites in the Cedar River, dispersal distance in the tributary was proportional to capture location expressed as a longitudinal distance to the creek mouth. Among the known immigrants, individuals captured in the upstream reaches and those produced by early-spawning parents were larger (Fig. 5). ANCOVA revealed statistically significant effects of both capture location (BY 2006: $F_{1,107} = 18.2, P < 0.0001$; BY 2007: $F_{1,188} = 52.6, P < 0.0001$) and maternal arrival date (BY 2006: $F_{1,107} = 4.9, P = 0.029$; BY 2007: $F_{1,188} = 13.0, P = 0.00039$). The models predicted that immigrants from the upper reaches were 6.1 mm and 10.3 mm larger than those in the lower reach in BY 2006 and 2007, respectively (Fig. 5).

**Discussion**

This study describes the dispersal of juvenile coho salmon in a population colonising newly accessible habitat. Data from BY 2003 and 2004, when sampling covered both the Cedar River and Rock Creek, revealed that maternal families occupied a large range of locations. Most families occupied several 500-m longitudinal bins along the river, and we frequently observed juveniles several kilometres away from the known or inferred spawning reach (Figs 2–4). These juvenile movements provided a secondary phase of dispersal following initial colonisation by adults and therefore contributed to the spatial expansion of the colonising population. Given the variation in habitat quality and rates of growth and survival in heterogeneous stream systems (Quinn & Peterson 1996; Ebersole et al. 2006), this dispersal might increase the probability of survival by at least some members of each family.

Although our estimates of dispersal distances were coarse, they exceeded most previous estimates from similar studies of stream salmonids in rearing habitats. Atlantic salmon (*Salmo salar*) and brook char (*Salvelinus fontinalis*) in streams have typically been found within several hundred metres of known or inferred nest sites (Webb et al. 2001; Einum & Nislow 2005; Einum et al. 2008; Foldvik et al. 2010; Hudy et al. 2010; Kanno et al. 2011). Importantly, compared with these studies, our sampling covered a greater spatial area and, in some cases, samples were collected later relative to hatching and emergence. Both of these differences increased our ability to detect longer-range dispersal. At the other extreme, stream-type Chinook salmon (*O. tshawytscha*) in the Columbia River system have been collected 10–100s of kilometres from spawning areas, although these fish may have been migrating to the ocean rather than rearing (Connor et al. 2001; Friesen et al. 2007). Our study involved a different species of salmonid, a different stream system and different densities compared with the other studies, so it is not possible to determine the reason(s) for differences in dispersal distance. We also could not determine why some families were more dispersed than others because of uncertainty over the precise location of the nest sites within spawning reaches and the range of dates over which samples from different families were collected. Regardless, the results are important because they reveal the large area over which families are distributed as a result of juvenile movement.

Several lines of evidence indicated a consistent and directed immigration of juvenile coho salmon from the mainstem Cedar River into and up its tributary, Rock Creek. First, densities within Rock Creek increased markedly from the summer to the fall (Table 2). Second, most adult coho salmon spawned in the Cedar River (this study, Anderson & Quinn 2007). Therefore, if the juveniles captured in Rock Creek had been produced there, they would have originated from very few families. This was not the case; 38–83% of adult females produced offspring captured in Rock Creek (Table 1). The large proportion of different families sampled in Rock Creek was striking and indicated that Rock Creek was not occupied by a few families spawned near the tributary mouth, but rather was a destination where unrelated individuals originating from many different nest sites converged.

The most direct evidence for tributary immigration came from the tagging data. For some families, we could confirm a maternal spawning location in the Cedar River based on radio- or PIT-tag detection data, and many juveniles from these families were captured in Rock Creek. The data from BY 2006 and 2007, when adult females were PIT-tagged, indicated that the majority of juveniles in the tributary were immigrants. Finally, some (5.9%) of the juvenile coho salmon PIT-tagged in the Cedar River were detected moving into Rock Creek. This indicated that the Rock Creek immigrants, while numerically dominating the tributary, may have only been a fraction of the total number of fish from the Cedar River.

Although tributary immigration had previously been observed in juvenile coho salmon, the timing of the movements observed here was novel. Previous studies of coastal systems found that tributary immigration occurred primarily during the fall or winter, and authors concluded that tributaries and wetlands offered refuge from high discharge encountered in the main river (Bustard & Narver 1975; Tschaplinski & Hartman 1983).
In contrast, the tributary immigration we observed had largely taken place by the time we sampled in late September or early October, and therefore, the fish entered in the spring or summer prior to fall–winter freshets. Once in the tributary, juvenile coho immigrants encountered a narrower stream with more defined pool-riffle structure, more woody debris and fewer large predatory rainbow trout (*O. mykiss*) than those in the main river (Kiffney et al. 2009). These habitat features may have encouraged immigrants to stay in Rock Creek after they entered, but temperature may have attracted them to it initially. The warmer temperatures in Rock Creek during the summer (mean ± SD for $N = 5$ pools in June–August 2008: 12.69 ± 2.23 °C) relative to the Cedar River ($N = 3$ pools, 10.49 ± 1.36 °C) would have been readily detectable at the confluence with the Cedar River.

Consistent with the condition-dependent hypothesis, juveniles dispersing further upstream in Rock Creek were larger than fish collected near the tributary mouth. Condition-dependent dispersal has been observed in many taxa (Bowler & Benton 2005), and the ability of juvenile salmonids to disperse increases through ontogeny (Einum et al. 2006). In the present study, we add that dispersal ability of juvenile salmonids is likely to vary substantially within a given cohort according to the range of body sizes observed in a population. Condition dependence is one of several nonmutually exclusive explanations for the observed dispersal patterns, including differences in habitat quality, predation and emergence timing; our results indicated that large fish were more capable of taking advantage of dispersal opportunities than small fish, at least within Rock Creek. Upstream movement is energetically demanding, and bigger fish have a greater metabolic capability and swimming performance (Brett 1995). Therefore, the upstream direction of movement likely increased the advantage of large size. We found no evidence for condition dependence in analysis of the BY 2003 and 2004 juveniles dispersing from known or inferred redd sites, perhaps because these fish primarily moved downstream in the Cedar River. In addition, fish from the Cedar River were collected over 2–4 weeks during the height of the growing season, and the confounding effect of accumulated growth during sampling may have obscured the analysis.

Several aspects of our results contradict the conventional paradigm that competitive exclusion governs movements of coho salmon. Previous research has emphasised subordinate social status and a failure to obtain and hold territories as a cause for downstream movements (Chapman 1962; Hartman et al. 1982; Nielsen 1992). In our study, this mechanism cannot explain widespread dispersal in a system with low overall densities, the consistent upstream movements in Rock Creek or the positive relationship between body size and dispersal distance in Rock Creek. Although competitive exclusion may regulate dispersal in established populations of coho salmon where space is limiting, forced emigration because of agonistic interactions is probably less common under the low densities typical of colonisation. Similarly, Kahler et al. (2001) found that habitat quality rather than subordinate body size explained coho salmon movements and that many fish moved upstream.

We suggest that the timing of emergence influenced dispersal. Previous work, both in this system (Anderson et al. 2010) and elsewhere (Einum & Fleming 2000), has shown that offspring of earlier-breeding females are larger at a given date. Thus, early-emerging individuals not only had more time for movements by a fixed sampling period later in the season, but also had the greater dispersal ability accompanying large size. Early-emerging individuals were probably the first individuals to move into previously unoccupied territories and thus may have enjoyed a prior residence advantage (e.g., Chandler & Bjornn 1988; Skoglund et al. 2012) in competition against later-arriving individuals. In Rock Creek, where end of summer densities in BY 2006 and 2007 approached values observed in established populations of coho salmon (Pess et al. 2011), later-arriving immigrants may have had difficulty acquiring foraging territories.

We cannot entirely separate cause from consequence regarding the relationship between body size and dispersal distance. In other words, fish dispersing to the upstream reaches of Rock Creek may have encountered favourable growing conditions upon arrival, contributing to their larger size. Our experience in Rock Creek suggests little difference between the lower and upper reaches in the physical habitat attributes relevant to growth of juvenile coho salmon. For example, residual habitat depth within our sampling pools (a strong predictor of coho salmon presence) was unrelated to the distance from the mouth of Rock Creek (Pess et al. 2011). The slightly warmer temperatures in the upper reaches (mean ± SD of $N = 3$ pools during June–August 2008: 12.88 ± 2.15 °C) may have provided a minor growth advantage relative to the area near the mouth ($N = 2$ pools, 12.40 ± 2.32 °C). More importantly, if juveniles sampled in the upper reaches were early immigrants to the creek, they likely encountered consistently lower conspecific densities than later arrivals captured downstream. We suspect that condition-dependent dispersal and density-dependent growth advantages acted synergistically, resulting in a substantial size difference between salmon sampled from the upper and lower reaches.
More generally, our results indicate that juvenile dispersal is an important component of the colonisation process. For species that deposit many embryos at a single location (e.g., many fishes and amphibians), a patchy breeding distribution could lead to density-dependent processes at small spatial scales (Einum et al. 2008). At the low abundances typical of colonising populations, juveniles are likely to be aggregated in a small number of nest sites and could significantly reduce their local density via dispersal. By enhancing per capita resource availability, dispersal may increase growth opportunities for individual fish (Einum et al. 2011) and consequently reduce exposure to size-selective predation and the likelihood of starvation. At the population level, this could increase survival and hence the rate of population growth during colonisation. Indeed, we observed much higher productivity by the coho salmon population than by the sympatric ocean-type Chinook salmon (Anderson 2011). The extended freshwater residence of juvenile coho salmon (typically one year) compared with ocean-type Chinook salmon (typically several months), as well as the ability of juvenile coho salmon to take advantage of high-quality rearing habitats above the dam through dispersal, may have contributed to this discrepancy.

For philopatric species, juvenile dispersal could catalyse adult colonisation. Dispersal during juvenile rearing may increase the propensity for individual salmon to ‘stray’ into non-natal habitats when they return to fresh water as adults (Hamann & Kennedy 2012). We have observed increased use of Rock Creek for spawning in recent years, and it seems plausible that adults who immigrated into the tributary as juveniles home to odours imprinted (sensu Dittman & Quinn 1996) in the creek rather the river. Such behaviour by second-generation, within-population recruits could be important for reaching the carrying capacity of high-quality rearing habitats if these areas are rarely settled by population immigrant adults that select breeding locations based on nest site characteristics. However, juvenile colonisation does not always lead to adult colonisation, as juvenile Chinook salmon often rear in non-natal tributaries (Murray & Rosenau 1989).

In a conservation context, our results emphasise the importance of maintaining connectivity for juveniles as well as adults. Construction of dams and other stream blockages, which eliminate habitat for migratory fish and fragment populations of resident species, poses a serious threat to aquatic diversity (Sheldon 1988; Morita & Yamamoto 2002; Limburg & Waldman 2009). Many structures, particularly culverts and small low-head dams, are likely to be partial barriers passable by larger fish that can sustain fast swimming speeds but not smaller fish with weaker swimming performance (Meixler et al. 2009). In this study, the widespread movements of juveniles and directed migration into the tributary indicate that barrier removal can effectively increase the range of rearing habitats, even when such areas are distant from breeding sites. If restoration planners focus exclusively on barriers to adults in selecting projects to increase stream connectivity, they may miss opportunities for increasing the quality and capacity of juvenile rearing habitats. For stream fish whose abundance is often limited by space, food and other resources for young, providing opportunities for juvenile spatial expansion may provide a significant conservation benefit.

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