Summer movement and growth of juvenile anadromous salmonids in small western Washington streams

Thomas H. Kahler, Philip Roni, and Thomas P. Quinn

Abstract: Movements of juvenile coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarki clarki*), and steelhead trout (*Oncorhynchus mykiss*) were studied by observations and recapture of marked individuals in three western Washington streams to test the hypotheses that few fish would move, downstream movement would predominate, movers would be initially smaller and grow slower after movement than residents, and habitat quality would influence movement. Contrary to predictions, from 28 to 60% of marked fish moved at least one habitat unit, and immigration of unmarked fish also indicated considerable movement. Upstream movement predominated but the stream with the step-pool/cascade channel type had fewer upstream movers and greater distances moved downstream. Coho movers were not smaller than nonmovers, as predicted based on assumptions that movement results from competitive exclusion. Habitat units that coho left were smaller and shallower but lower in density than units where coho remained. Thus, movement is a common phenomenon rather than an aberration, and may reflect habitat choice rather than territorial eviction. Moreover, movers grew faster than nonmovers, so the "mobile fraction" of the population was not composed of competitively inferior fish but rather individuals that thrived. The phenomenon of small-scale habitat- and growth-related movements should be considered when planning and interpreting studies of juvenile salmonid ecology in streams.

Résumé : Les déplacements des juvéniles du Saumon coho (*Oncorhynchus kisutch*), de la Truite fardée (*Oncorhynchus clarki clarki*) et de la Truite arc-en-ciel (*Oncorhynchus mykiss*) anadrome ont pu être suivis grâce à l'observation et la recapture d'individus marqués dans trois cours d'eau de l'ouest du Washington afin d'éprouver les hypothèses selon lesquelles peu de poissons se déplacent, les mouvements vers l'aval prédominent, les poissons mobiles sont au départ plus petits et, une fois déplacés, ils croissent plus lentement que les poissons sédentaires et, finalement, la qualité de l'habitat influence les déplacements. Contrairement aux prédictions, de 28 à 60% des poissons marqués se sont déplacés d'au moins une unité d'habitat et l'immigration de poissons non-marqués reflétait l'existence de nombreux mouvements. Les déplacements vers l'amont prédominaient; cependant, dans le cours d'eau où il avait une succession de seuils et de fosses et des cascades, moins de poissons migraient vers l'amont et les distances parcourues vers l'aval étaient plus grandes. Les Saumons coho mobiles n'étaient pas plus petits que les sédentaires, contrairement aux prédictions qui assumaient que les déplacements étaient dus à l'exclusion par compétition. Les unités d'habitat abandonnées par les Saumons coho étaient plus petites et moins profondes que celles où les saumons restaient sur place et leur densité était moindre. Ainsi, les déplacements sont des phénomènes courants plutôt que des événements aberrants et ils reflètent peut-être un choix d'habitat plutôt que l'éviction d'un territoire. De plus, les poissons mobiles croissent plus rapidement que les sédentaires; la « fraction mobile » de la population ne se compose donc pas de poissons inférieurs face à la compétition, mais plutôt de poissons gagnants. Le phénomène des déplacements à petite échelle reliés à l'habitat et à la croissance doit être pris en considération dans la planification et l'interprétation d'études sur l'écologie de saumons juvéniles dans les cours d'eau.

[Traduit par la Rédaction]

ıtroduction

Movement is among the most important behavioral patıns of animals, as it allows them to respond to physical ıd biological conditions in their environment to increase eir growth, survival and reproductive success. These movements occur over many scales of space and time, and may occur as individual responses to proximate conditions or as evolved responses by the population or species (Dingle 1996). Although some species undertake spectacular long-distance migrations, many animals move or disperse in a less directed and synchronized manner. These movements may be on eco-

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Table 1. Stream characteristics.

Stream characteristic	Big Beef Creek	Shuwah Creek	East Fork Griffin Creek
Gradient	0.8%	2%	5.7%
Bankfull width (m)	15	6.5	5.5
Habitat unit length (m)	15.7	6.9	3.8
Channel classification	Forced pool-riffle	Forced pool-riffle	Step-pool/cascade
Max. discharge (1998 study) ($m^3 \cdot s^{-1}$)	0.27	0.09	0.1
Density (salmonids·m^{-2})	0.22 (1997) 0.87 (1998)	0.33	0.31
Pool area	75% (1997) 61% (1998)	55%	54%
Riffle area	25% (1997) 39% (1998)	36%	46%

Note: Gradient, Bankfull width, and Mean density are the means for each study section. Habitat unit length is the average length of habitat units in each study section. Channel classification from Montgomery and Buffington (1997). Max. discharge is the maximum discharge (estimated for Shuwah Creek and East Fork Griffin Creek; U.S. Geological Survey data for Big Beef Creek) during the 1998 study period, which was the period between fish marking and recapture. Pool area and Riffle area are the percentages of the total area of each study section. "Riffle" includes cascades. Glides were not included.

periods ranged from 0.27 to 0.16 $m^3 \cdot s^{-1}$ in 1997 and from 0.26 to 0.10 $m^3 \cdot s^{-1}$ in 1998.

In 1998, Griffin Creek and Shuwah Creek were also studied. Griffin Creek is a tributary of the Snoqualmie River, which flows into central Puget Sound. The study section was located on the East Fork of Griffin Creek, in a high-gradient (5.7%) confined reach, with 5.5-m average bankfull width and angular boulder and cobble substrate (see Table 1). This study section was the highest-gradient channel located that was utilized by coho salmon and also satisfied our other stream-selection criteria. The upper and lower ends of the section were step-pool channels and the steeper middle part of the section was a cascade channel. Stream discharge during the summer ranged from 0.10 $m^3 \cdot s^{-1}$ to near zero when the lower portions of the study section went dry in late August. The riparian zone was well shaded by second-growth conifers with deciduous streambank vegetation. Large wood was sparse within the wetted channel and streambank vegetation provided little overhead cover; prey refuge habitat consisted primarily of interstitial spaces between substrate elements.

Shuwah Creek is a tributary of the Soleduc River near Forks, Clallam County, Wash. Bankfull width of the study section was 6.5 m and the incising, moderately confined channel was forced pool-riffle type with gravel and cobble substrate (see Table 1). Summer discharge ranged from 0.09 $m^3 \cdot s^{-1}$ to near zero when the lower portion of the study section ceased flowing in early September. Vegetation within the study section consisted of second-growth conifers, with dense overhanging salmonberry (*Rubus spectabilis*) on the banks. Abundant large wood, undercut banks, and overhanging vegetation provided prey refuge habitat.

These three streams were selected because they represented a range of channel types and gradients, and had the same salmonid species. All three streams contained age-0+ coho salmon, and age-0+ and 1+ steelhead and cutthroat trout. Given the close proximity of the study streams to marine waters and the length-frequency distributions of captured fish, all salmonids were assumed to be anadromous. No age-2+ steelhead were observed in any stream, and few age-2+ cutthroat trout were observed: one each year in BBC, four in Shuwah Creek, and none in Griffin Creek. Common predators in the three streams included sculpins (*Cottus* spp.), belted kingfishers (*Megaceryle alcyon*), great blue herons (*Ardea herodius*), river otters (*Lutra canadensis*), and raccoons (*Procyon lotor*).

The study streams are all subjected to a maritime climate regime characterized by mild wet winters and summer drought. All of the streams are below elevations that have continuous winter snow; precipitation falls almost entirely as rain in the study subbasins. In contrast with streams under continental climate regimes, maximum discharge events typically occur between November and March in the study streams.

Study design

The basic study design in all three streams was to capture all salmonids within a defined study section, measure and individually mark each fish, follow their movements throughout the summer using periodic snorkel surveys, and recapture individuals in the fall to obtain final measurements. Habitat units where fish were captured were measured (slope, area, and residual depth) and classified as riffles, pools, glides, or cascades. Movement could thus be related to species, initial size, growth rate, density, and habitat features. We marked fish using the photonic marking system developed by NEWWEST Technologies, Santa Rosa, Calif. This system consists of a modified mass-inoculation gun powered by compressed CO_2, which injects marking fluid composed of pigmented latex microspheres suspended in deionized water (with the appearance of low-viscosity paint). Fish were marked in the dorsal fin, upper and lower lobes of the caudal fin, and anal fin. With this method, hundreds of individuals could be uniquely identified with marks discernable to a snorkeler (Kahler 1999). Although not specifically tested, no behavioral differences between marked and unmarked individuals were observed.

We collected and marked salmonids in BBC between 25 July and 6 August 1997. Blocking nets were placed at both ends of each habitat unit and fish were captured with pole seines using three-pass removal. The pole seines were seine nets of various dimensions with mesh sizes of approximately 3 mm, with 1.8-m long wood dowels attached at each end to facilitate maneuvering of the net. Captured fish were anesthetized with MS-222, identified as coho or trout, measured to the nearest millimeter (fork length) and weighed to the nearest 0.1 g. Salmonids 45 mm and larger were individually marked and all fish were returned to the habitat unit where they were captured. We conducted snorkel surveys on 15 and 22 August, 4 and 7 September, and 22 October 1997 to locate marked individuals by habitat unit. In addition, on 26–29 August and 21–23 September, fish within the study section were sampled using pole seines, identified, measured, weighed, and released into the habitat unit where they were recaptured.

In addition to the snorkeling, in July 1997 we bounded a 331-m study section of BBC with weirs with two-way fish traps to intercept all fish moving into and from the study section. Weirs were V-shaped, and constructed of 0.9 × 2.4 m wood-frame panels of 6-mm mesh hardware cloth, with the "V" opening upstream. At the

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logically important spatial scales (e.g., a change in habitat) even though the absolute distance moved may not be great (Swingland and Greenwood 1984; Dingle 1996). Important questions regarding movement include the following: do most individuals move or only a few; do individuals move because they are in inadequate habitat or because they cannot compete in high-quality habitat, and; what are the fitness consequences of movement?

The empirical study of animal movement often depends on documenting the distribution of animals of known origin. Typically, this is done by marking and later searching for individuals within a defined study area. Animals that move are less likely to be detected than those that do not (Koenig et al. 1996), and this leads to biased (under)estimates of movement and tends to lead to the neglect of the possible fitness benefits of movement. Owing to the importance of salmonid fishes (genera *Oncorhynchus*, *Salmo*, and *Salvelinus*) in recreational and commercial fisheries and as components of regional biodiversity, extensive research has been conducted on their movements. Because of this extensive research, salmonids provide a good opportunity to test hypotheses about movement. These fishes display classic migrations, the exodus of juveniles (smolts) to the ocean (Iwata 1995) and return of maturing adults to their natal stream (Dittman and Quinn 1996), as well as exhibiting dispersal movements of juveniles in freshwater (reviewed by McCormick et al. 1998).

Studies of the habitat use and movement patterns of juvenile anadromous salmonids in coastal North American streams have indicated two major movement events prior to seaward migration: the dispersal of fry following emergence in the spring and early summer and the movement of parr to low-velocity or off-channel rearing areas in the fall and winter. Research in coastal systems has generally concentrated on the spring or (especially) fall periods, and information on the movements of juvenile anadromous salmonids during the summer, following their initial dispersal but prior to their fall redistribution, is sparse. Studies have indicated that few juveniles move during summer relative to the numbers moving during the spring dispersal and fall redistribution events (e.g., Hartman and Brown 1987). These patterns are best documented in coho salmon (*Oncorhynchus kisutch*), the most abundant juvenile salmonid in most coastal streams accessible to anadromous fishes. This species typically spends one full year in freshwater (or more in the northern end of its range) prior to seaward migration and tends to occupy pool habitats (Sandercock 1991).

Unlike the studies on coastal populations, recent studies of age-1+ and older salmonids in small, high-elevation streams subject to continental climate regimes have shown considerable movement in summer (Gowan and Fausch 1996; Young 1996). This is in contrast to the "restricted movement paradigm" (RMP) that has been generally accepted within the fisheries community (Gowan et al. 1994). The RMP holds that salmonids in streams generally occupy small home ranges that they seldom leave. Gowan et al. (1994) challenged the RMP and asserted that many studies claiming to support the RMP were unlikely to detect movement and often made claims of limited fish movement based on the recapture of only a small fraction of marked individuals. Studies designed under the assumption that fish are likely to move have often yielded results that contradict the RMP (e.g., Young 1996). Differences in observed movement among salmonid populations may be attributable to differences in the designs and techniques of respective studies (Young 1996) and to intrinsic differences in the habitats or ecology of the fishes. One may expect less upstream movement in high-gradient streams, for example, but many studies of movement do not report gradient. Despite strong evidence against the RMP from continental populations of salmonids, there is a lack of evidence against restricted summer movement in coastal populations of juvenile anadromous salmonids.

Movement of juvenile anadromous salmonids prior to seaward migration is generally believed to be a response to poor or declining habitat conditions, evidenced by a negative relationship between pool area and movement (Bilby and Bisson 1987). Fish may move in response to interrelated factors including aggressive interactions (Chapman 1962), changes in discharge or temperature (Bjornn 1971), or decreasing food abundance (Wilzbach 1985). Declining stream discharge shrinks available habitat, increasing density. The incidence of agonistic behavior increases with density (to a point) and competitively inferior fish may move downstream (Chapman 1962; Titus 1990).

To the extent that movement is a response to saturated habitat, individuals that move are expected to be smaller and grow slower than fish that do not move. Smaller individuals are competitively inferior, and prior residency provides a competitive advantage (e.g., coho salmon, Rhodes and Quinn 1998; steelhead trout, *Oncorhynchus mykiss*, Abbott et al. 1985). A small fish that loses a competitive interaction and moves to another habitat may encounter prior residents and be forced to accept marginal habitat or continue moving. Alternatively, individuals may leave low-density, poor-quality habitat and encounter unoccupied high-quality habitat, where they experience high growth rates, which could increase survival at subsequent life stages (Quinn and Peterson 1996). However, the fate of salmonids that move is seldom known. Accordingly, we investigated the summer movements of individually marked anadromous, age-0+ coho salmon, and age-0+ and 1+ cutthroat (*Oncorhynchus clarki clarki*) and steelhead trout in three coastal streams of Washington State, U.S.A., and tested the following hypotheses: (*i*) mobile fish within a population represent a small minority; (*ii*) movement is predominantly downstream; (*iii*) mobile fish are initially smaller than sedentary fish; (*iv*) mobile fish grow more slowly than sedentary fish, and; (*v*) fish more often move away from low-quality than high-quality habitat.

Materials and methods

Study sites

Big Beef Creek (BBC), studied in 1997 and 1998, flows into the east side of Hood Canal, Wash. At the study section, about 1 km above tidewater, the bankfull width was approximately 15 m, and the gradient was 0.8% (Table 1). The channel type was forced pool-riffle (channel classifications from Montgomery and Buffington 1997) with a gravel and cobble substrate. The study area was logged approximately 100 years ago, and the riparian vegetation is now predominantly deciduous, with second-growth conifers also present. The riparian canopy provides incomplete coverage of the broad, aggrading channel, with bank vegetation providing limited overhead cover for fish. Discharge during the summer study

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apex of the "V," a 10-cm diameter ABS (acrylonitrile-butadiene-styrene) pipe conveyed fish downstream into a trap. The Washington Department of Fish and Wildlife (WDFW) required that water velocity at the screens be minimized to prevent impingement of juvenile fish, so a dam was constructed downstream of the screens. Fish moving upstream were directed into an upstream trap at a notched opening on the dam. We checked the traps daily, usually morning and evening, from 21 July until 16 September 1997, when a freshet destroyed the weirs. Fish in the traps were measured and identified, checked for marks, and released in the direction that they were traveling. Starting on 1 August 1997, fish entering the study section were given right or left pelvic fin clips (following Gowan and Fausch 1996) designating their direction of movement.

In 1998, we repeated the snorkeling study on BBC but the addition of similar marking and snorkeling on Griffin and Shuwah creeks precluded operation of the weir and traps on BBC. We made no recapture efforts until the end of the study in 1998, and we extended snorkel surveys upstream and downstream of the study sections to account for fish that had moved beyond section boundaries, in part to compensate for the lack of trapping.

On BBC in 1998, the study section (where fish were marked) was 184 m with the downstream end in the approximate location of the 1997 downstream weir. We began fish collection and marking on 15 June 1998 using the same methods as in 1997, except that trout older than age-0+ were identified to species. We measured and numbered habitat units in the study section and in two sections extending 163 m upstream of and 230 m downstream of the study section. We conducted weekly snorkel surveys of all sections (577 m) from 7 July to 15 September 1998, and recaptured fish from 16–18 September 1998 in the study section and all other units where marked fish were observed on 15 September.

In Griffin Creek, we collected fish for marking in a 119-m-long study section on 23–24 June 1998, following the same procedures as in BBC in 1998 except that three-pass electrofishing was used rather than pole seining. We measured and numbered habitat units in the study section and for 32 m upstream, and 111 m downstream of the study section. We had cataloged habitat units over 100 m upstream of the study section, but beyond 32 m, a cascade dewatered within three weeks, isolating upstream units. We conducted weekly snorkel surveys of the study, and upstream and downstream sections (262 m) from 16 July to 19 August 1998 when the study section consisted of mostly isolated pools with a few habitat units still connected by flowing water. We recaptured fish on 21 August 1998 via electrofishing starting 111 m downstream of the study section, and continuing to the upstream end of the study section. The stream was dry upstream of the study section for hundreds of meters and had been since early August.

On Shuwah Creek, we divided a 301-m study section into three subsections: a 98-m downstream subsection and an 84-m upstream subsection where fish were marked, and an intervening 119-m subsection where no fish were marked. The study section was configured in this manner to accommodate the design of a concurrent companion study. We collected fish within the upstream and downstream subsections for marking on 1–3 July 1998, using three-pass electrofishing as in Griffin Creek. We numbered and measured habitat units within the study section, and 120 m upstream and 178 m downstream of the study section. We conducted weekly snorkel surveys of all sections (599-m total) from 14 July to 31 August 1998 and recaptured fish on 6–8 September 1998 in the study section and all other units where marked fish were previously observed.

We would have preferred to use electrofishing in all streams but WDFW would not permit electrofishing in BBC. Fortunately, BBC was well suited for seining; most of the habitat units were large and structurally simple. The large pools that had complex features such as woody debris jams would have proven challenging for electrofishing, considering the large volume of water and complexity of escape cover. Both coho salmon and cutthroat trout were easily collected by seining because of their tendency to forage high in the water column of pools. Steelhead were also readily captured in BBC and were a larger fraction of the total catch there than in the other streams.

Wiley and Tsai (1983) compared electrofishing and seining in small streams and concluded that the "...electroshocker was more effective than seines for making quantitative collections." However, we were not conducting population estimates but collecting fish for marking, and made inferences only on fish recaptured or observed by a snorkeler. Presumably, marked fish would be equally observable by a snorkeler, regardless of initial capture method at marking. Seining undoubtedly affected recapture efficiency in BBC but would not have introduced a bias toward the capture of either movement class (as defined below). While it is possible that sampling technique could have introduced some behavioral artifact, there were other differences among streams that also could have done so. Any bias towards density resulting from differences in capture technique could not be determined; both the lowest density (1997) and the highest density (1998) observed during the study were in BBC. Such a possible bias was considered by the inclusion of "stream" as a variable in statistical analyses.

For data analysis, we classified all marked fish either observed during snorkel surveys or recaptured as "recovered". We called fish recovered in a habitat unit other than where they had been marked or previously located "movers". We called fish that were recovered in their original habitat unit "nonmovers". The term nonmovers was not intended to imply that fish had not moved, only that we had not detected their movements. Both weekly snorkeling and final recapture efforts were during daylight hours, thus we would have failed to detect movements occurring on a smaller time scale, such as the diel changes in habitat use reported by (Hilderbrand and Kershner 2000).

We calculated the specific growth rates (μ: ln(mm)·day^{-1}) of recaptured individuals in each stream from Ricker (1979)

$$\mu = (\ln L_t - \ln L_0)/\Delta t$$

where L_t is the final length (mm) recorded at recapture, and L_0 is the initial length (mm) recorded at marking, and Δt is the growth period in days between marking and recapture.

We selected as surrogates of habitat quality two physical variables, residual depth and area, and one biological variable, salmonid density, to determine whether habitat influenced fish movement or growth. We selected density as a variable because it provides a measurable indicator of the intangible factor competition. We defined residual depth as the maximum depth of a habitat unit, minus the maximum depth at the hydraulic control (the downstream streambed feature that creates the lip of the pool) of that unit. We calculated area by multiplying the unit's length by its average width. We defined density as the number of salmonids (all species) per unit area at the time of marking. For comparison, higher-quality habitat units would have greater area and residual depth and lower density (less competition) than lower-quality habitat units. We used the number of habitat units traversed by a mover for analysis of movement distances because the differences in channel types, sizes, and gradient made it inappropriate to compare the number of meters moved by individuals in the three streams. For example, because of the among-stream differences in size of habitat units, a fish could move 10 m in BBC without leaving its habitat unit whereas a fish might traverse 2–3 habitat units with a 10-m movement in Griffin Creek. Thus, a measure of the number of habitat units traversed provided a more ecologically meaningful comparison among streams than did the number of meters moved.

Multiple observations provided chronological records of movement as well as initial and final location. However, some individuals moved both upstream and downstream during the study, making their categorization as either upstream or downstream movers ambiguous, especially if they returned to and were finally recaptured

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Table 2. Numbers of marked fish, recovered fish (i.e., recaptured or snorkel observation), and movers (i.e., fish observed to have moved at least one habitat unit from where they were marked) in each stream by species.

Salmonids	BBC 1997	BBC 1998	Griffin	Shuwah
Marked				
Total	707	501	107	141
Coho	231	434	82	67
Cutthroat	31	12	22	47
Steelhead		39	2	9
Trout fry	445	16	1	18
Recovered				
Total	247	104	55	101
Coho	99	87	44	59
Cutthroat	10	3	11	24
Steelhead		13	0	6
Trout fry	138	1	0	12
Movers				
Total	115	29	33	55
Coho	40	24	26	29
Cutthroat	4	2	7	15
Steelhead		3	0	3
Trout fry	71	0	0	8

Note: Trout fry were age-0+ trout that were not identified to species. Cutthroat and steelhead trout were age-1+ and age-2+ (six total in all streams), and were not differentiated in BBC during 1997. BBC = Big Beef Creek.

at their original marking location. Accordingly, we used a count of the total number of upstream and downstream movement events by all fish in each stream to indicate directional movement patterns. Analysis using each movement event treats repeated movements by individuals as independent, which they are not, although they took place from different habitat units and were separated by significant periods of time. Therefore, statistical analyses using the number of movement events were repeated using the number of moving individuals, and results of both tests are noted.

Although marked steelhead and cutthroat trout were recovered in all streams, sample sizes, species, and age composition of trout varied greatly among streams. Because salmonids differ in habitat use among species and age groups (e.g., Bisson et al. 1988), we conducted most analyses using only coho salmon data with the exception that "density" always refers to the number of salmonids (all species) per square meter. Throughout the paper, we will indicate when results or discussions apply to all salmonid species or to only coho.

We used χ^2 tests to compare proportions of movers and nonmovers, and direction of movement within and among streams. We used an analysis of variance (ANOVA) blocked by stream to compare differences in length and growth rate between movers and nonmovers, and between upstream and downstream movers. We used Tukey multiple comparisons for post-hoc analyses of ANOVA and χ^2 tests. We used logistic regression to examine the relationship between movement and habitat characteristics. For all tests, we considered $P \leq 0.05$ indicative of significance.

Results

In 1997, 707 juvenile salmonids were individually marked in BBC, and 749 juvenile salmonids were marked in Big Beef, Griffin, and Shuwah creeks combined in 1998 (Table 2). Location data were collected on 247 (35% of marked) fish in 1997 and 260 (35% of marked) fish in 1998. We rejected the hypothesis that mobile fish within the population represented a small minority. Movers (all species) comprised 47% of the recovered fish in 1997 and 28–60% of the recovered fish in 1998, depending on the stream (Fig. 1), and 14–36% of the movers moved more than once (Table 3).

More upstream than downstream movements (included coho salmon and trout) were recorded in almost all cases (BBC 1997, 51%; BBC 1998, 72%; Shuwah, 59%; Griffin, 45%), although only in BBC in 1998 did the numbers of upstream and downstream movements differ significantly from a 50:50 ratio (χ^2 test; $P < 0.01$). Similar results (BBC 1997, 53%; BBC 1998, 89%; Shuwah, 63%; Griffin, 45%) were obtained using net displacement data (i.e., comparing final recapture location to marking location, ignoring intervening movements). Further analyses were conducted using only coho salmon data, with the exception that "density" always refers to the number of salmonids (all species) per square meter.

The initial lengths of coho salmon differed among streams but the initial lengths of movers and nonmovers did not significantly differ within streams ($P = 0.808$; Table 4). Within-stream differences in mean initial lengths of upstream and downstream movers were not significant ($P = 0.628$), but movers grew faster than did nonmovers ($P = 0.031$; see Table 4).

The mean distances (measured in habitat units) moved upstream by coho salmon were similar to the downstream distances in all streams except Griffin Creek, where they moved over four times farther downstream than upstream ($P < 0.001$; Table 5). Post-hoc multiple comparisons (Tukey Honestly Significant Difference) indicated that the mean distance in Griffin Creek differed from the mean distances in BBC in 1997 and 1998, and Shuwah Creek ($P = 0.006$, $P < 0.001$, $P = 0.001$, respectively), but distances moved in BBC and Shuwah did not differ from each other. The proportions of upstream and downstream movements by coho salmon differed among streams (χ^2 test; $P < 0.005$, see Table 5). The lowest proportion of upstream movement was observed in Griffin Creek (45%) and the highest proportion was in BBC (56% in 1997 and 68% in 1998), but this overlapped with Shuwah Creek (56%).

We used multiple logistic regression to evaluate the relative roles of physical habitat and density on the likelihood of movement by coho salmon. Our initial analysis included coho that did not move and all movement events by those that moved, for a total of 317 complete observations. The habitats from which fish moved were smaller in area (59.4 m^2 vs. 95.2 m^2; $p = 0.029$) and depth (0.50 m vs. 0.64 m; $p = 0.007$) than those where the fish stayed (see Table 4). Paradoxically, the habitats from which fish moved had lower densities (0.57 fish·m^{-2} vs. 0.73 fish·m^{-2}; $p = 0.002$) than the habitats where they remained, thus the fish tended to leave small habitat units despite lower densities. Stream was entered into the model as a "dummy variable", but was not significant ($p = 0.71$), indicating that the patterns were consistent among sites. Because of our concern for the violation of the data-independence assumption when using movement events as the dependent variable (noted above), the logistic regression was repeated using only the first move by each fish (ignoring subsequent moves by those individuals). This reduced the sample to 268 individuals but

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Fig. 1. The percentages of recovered juvenile salmonids and movers in Big Beef Creek in 1997 and 1998 (BBC 1997 and BBC 1998) and Griffin and Shuwah creeks in 1998. The pie charts on the left show the total number of marked fish (*N*) in each creek. "Missing" is the percentage of marked fish not recovered; "Recovered" fish were either observed by a snorkel survey or captured. The charts on the right show the proportions of recovered fish that moved at least one habitat unit from where they were marked (Movers) and that remained in the original unit (Nonmovers).

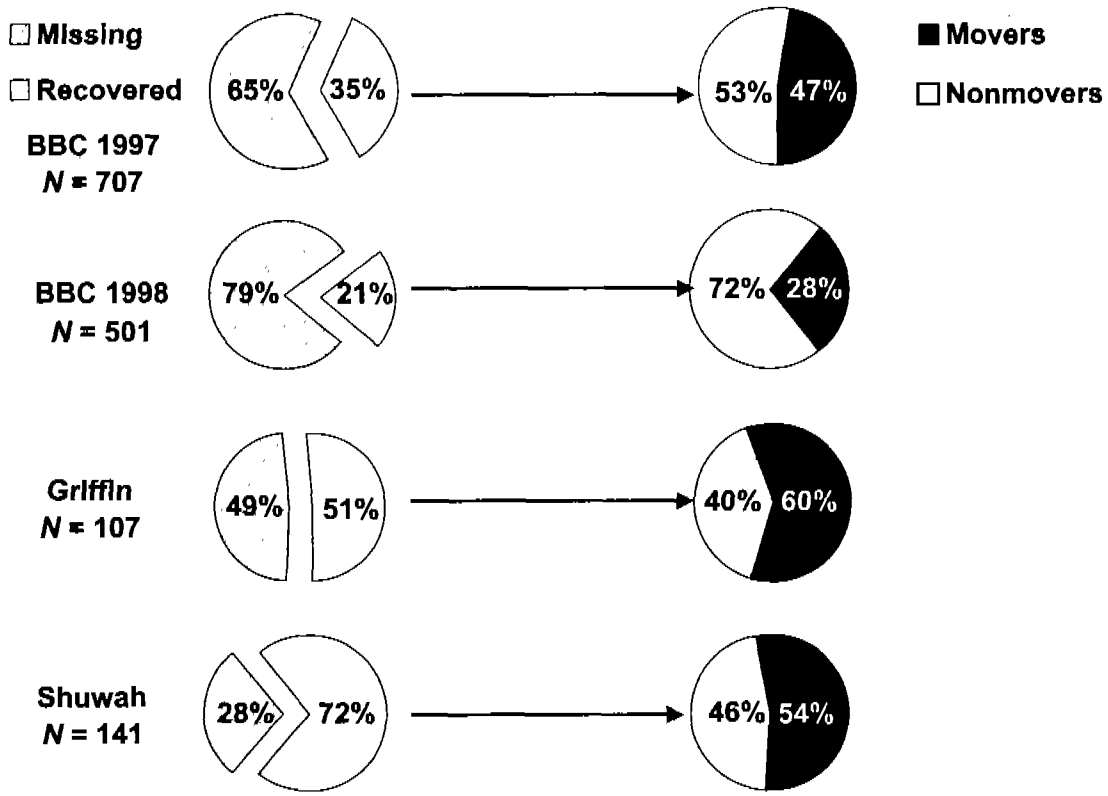

Table 3. The numbers (and percent, in parentheses) of fish moving one or more times per summer in Big Beef Creek (BBC), Griffin Creek, and Shuwah Creek.

Creek/year	1 move (%)	2 moves (%)	3 moves (%)	4 moves (%)	Movements-to-fish ratio
BBC/1997	79 (77)	22 (21)	2 (2)	0	1.25
BBC/1998	25 (86)	2 (7)	2 (7)	0	1.21
Griffin/1998	27 (82)	4 (12)	2 (6)	0	1.24
Shuwah/1998	35 (64)	16 (29)	3 (5)	1 (2)	1.45

Note: The movements-to-fish ratio represents the number of movement events observed in each creek divided by total number of individual fish that moved.

produced broadly similar results. There were significant effects of depth (0.51 m vs. 0.65 m for fish that moved and stayed, $p = 0.004$) and density ($p = 0.026$), but not area ($p = 0.086$) or stream ($p = 0.58$).

Discussion

Percentages of mobile fish within the populations

Rather than being a small minority within the populations, movers represented from 28 to 60% of the recovered fish within the study streams and 14 to 36% of them moved more than once. Thus, movement from one habitat unit to another represented common behavior for these salmonid populations. Further evidence for the prevalence of movement, albeit indirect, comes from the incidence of unmarked fish in the study sections of Griffin and Shuwah creeks. The number o unmarked fish in the study sections increased from 23 fol lowing marking to 203 at recapture in Shuwah Creek an from 7 to 62 in Griffin Creek, despite the fact that 18 of th 31 habitat units were either dry or devoid of fish at the tim of recapture in Griffin Creek. This nearly ninefold increas in unmarked fish due to immigration indicated highly mo bile fish populations.

In all streams, the number of marked fish observed de clined over time, especially in BBC in 1998. One possibl explanation for this decline is loss of marks. Mark qualit was variable and in some cases declined over time eventu ally becoming unreadable. However, usually only one or tw of the four marks faded and even when the colors becam indistinguishable, it was obvious that the fish had been markec

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Table 4. Coho salmon initial lengths (mm) of nonmovers and movers and of upstream and downstream movers; growth (ln mm·day^{-1}) of nonmovers and movers; mean density (salmonids·m^{-2}), residual depth (cm), and area (m^2) of habitat units from which coho moved or remained.

Comparison	BBC 1997	BBC 1998	Griffin	Shuwah
Initial length				
Nonmovers	71 (6.7) [59]	58 (7.6) [63]	58 (8.0) [18]	68 (12.3) [30]
Movers	70 (5.9) [34]	59 (6.4) [24]	60 (8.3) [26]	66 (13.1) [29]
Upstream	69 (6.2) [20]	60 (5.8) [21]	60 (10.1) [14]	67 (14.2) [23]
Downstream	72 (4.4) [16]	61 (6.9) [10]	59 (6.9) [17]	67 (14.5) [18]
Growth ($\times 10^{-3}$)				
Nonmovers	2.01 (0.97) [9]	Insufficient data	0.91 (0.74) [8]	1.36 (0.75) [15]
Movers	2.90 (1.06) [19]		1.35 (0.63) [4]	1.96 (1.25) [15]
Mean density				
Nonmovers	0.42 (0.21) [59]	1.19 (0.43) [65]	0.65 (0.19) [22]	0.38 (0.11) [29]
Movers	0.42 (0.23) [36]	1.12 (0.49) [30]	0.50 (0.27) [33]	0.39 (0.16) [50]
Habitat depth				
Nonmovers	78 (3.1) [59]	67 (1.5) [65]	23 (0.5) [21]	59 (2.3) [29]
Movers	66 (3.6) [35]	53 (2.0) [30]	21 (0.6) [29]	54 (2.0) [50]
Habitat area				
Nonmovers	160 (100) [59]	88 (49) [65]	20 (5) [18]	36 (16) [29]
Movers	131 (74) [36]	61 (36) [30]	16 (7) [34]	36 (17) [50]

Note: Parentheses indicate standard deviations; brackets indicate sample sizes.

Table 5. Mean upstream and downstream distances (measured in number of habitat units and in meters) moved by coho salmon movers in each stream (standard deviations in parentheses), maximum distances moved in each direction, and the proportions of movements that were upstream, expressed as the percentage of all coho salmon movements from the point of capture or previous observation.

Comparison	BBC 1997	BBC 1998	Griffin	Shuwah
Distance upstream				
Units moved	3.6 (3.6)	4.4 (3.6)	2.5 (2.8)	6.4 (7.9)
Meters moved	46.5 (10.9)	42.8 (8.2)	9.8 (9.6)	42.2 (14.2)
Maximum (m)	234	125	39	213
Distance downstream				
Units moved	5.8 (6.7)	3.0 (3.0)	11.0 (14.1)	5.2 (5.6)
Meters moved	50.5 (15.3)	21.6 (3.3)	43.4 (57.4)	26.3 (5.6)
Maximum (m)	178	142	201.5	163
Proportion upstream	56%	68%	45%	56%

Note: BBC = Big Beef Creek.

Thus, a recovered fish with an illegible mark was counted as a marked fish, although no analysis on individual attributes was possible. We therefore discount mark loss as an explanation for the decline in marked fish.

Two other factors that might contribute to the decline of marked fish over time are emigration and mortality. The weirs on BBC in 1997 indicated that only 1% (7 fish) of the marked fish moved from the study section. Despite this low number of emigrants from the study section and frequent sampling, only 29% of the marked fish were recaptured at the end of the study, and an additional 4% were confirmed mortalities over the course of the summer. Allowing for some capture inefficiency, this would indicate that the fish population in BBC in 1997 experienced a mortality rate generally consistent with rates estimated (49%; Nickelson et al. 1993) for coho salmon elsewhere. A high mortality rate has been cited as evidence for limited movement in cases where only a few marked fish were recovered (see discussion in Gowan et al. 1994). In the present study, the decline in marked fish over time appears to have resulted from a combination of high mortality with substantial small-scale but limited large-scale movement.

Direction of fish movement

The prediction that summer movement would be predominantly downstream originated from observations that aggressive interactions force competitively inferior members of a coho salmon population of to emigrate (e.g., Chapman 1962), and that the directional nature of streams might cause displaced individuals to move downstream. This hypothesis was summarized by Titus (1990) as follows: Large, dominant fish with high growth potential have territories that expand as they grow, and these dominant fish force smaller fish with lower growth potential to move downstream.

Support for the expectation of downstream movement by age-0+ anadromous salmonids can be found in the literature for coho salmon (Hartman et al. 1982) and chinook salmon (Bradford and Taylor 1997). However, this contrasts with the

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predominance of summer upstream movement in populations of age-1+ and older salmonids in the Rocky Mountains (Gowan and Fausch 1996) and brook trout (*Salmo fontinalis*) in Idaho (Adams et al. 2000). In the present study, movements were not predominantly downstream. More movements were upstream than downstream in all streams except Griffin Creek, where 45% of the movements were upstream.

Previous studies (e.g., Peterson 1982) also reported that juvenile coho and cutthroat moved upstream but they provided only counts of the number moving through traps over a given period, not proportions of the population. We were able to consider the total number of observed movement events by all fish in each stream rather than the numbers of mobile fish (movers) because the frequent snorkeling observations allowed multiple observations per fish. For example, had only marking and final recapture data been considered (ignoring intervening movements detected by snorkeling), we would have missed 36% of the movement in Shuwah Creek. However, analysis of our data using only marking and final recapture locations (i.e., one data point per fish) supported similar conclusions to those based on all movement events; there was more movement upstream than downstream in all streams except Griffin Creek (45% upstream).

While many fish in our study streams moved once in only one direction, some moved more than once and in both directions and several returned to their original marking location. The complex movement patterns we observed suggested that juvenile salmonids may engage in "exploratory" movement behavior as discussed by Smithson and Johnston (1999) for non-salmonids in Little Glazypeau Creek, Ark. Similarly, Armstrong et al. (1997) reported that Atlantic salmon parr showed three behavior patterns in an experimental stream: some settled immediately and did not move, some explored the available habitat extensively and then settled, and some never settled but moved throughout the stream section.

Fish size, movement, growth, and habitat quality

The hypothesis that coho salmon movers would be initially smaller than sedentary fish was based upon the assumption that movement would result primarily from size-biased competitive interactions (Chapman 1962; Rhodes and Quinn 1998), but our results did not support this hypothesis. Movers were also expected to grow slower than sedentary fish under the assumption that movers would be intruding into territories held by others and so would have a competitive disadvantage (Rhodes and Quinn 1998) but the movers grew faster than nonmovers. Perhaps competitive interactions were not the primary motivation for summer movement in our study streams.

We examined the movements of age-0+ coho salmon, whereas the studies that formed the basis for the hypotheses concerning size and growth examined aggressive interactions or foraging behavior and growth. For example, Nielsen's (1992) observations of coho salmon foraging behavior and growth were based primarily on fish that remained in their original habitat unit but 40–73% of the marked fish left their original habitat unit. Nielsen (1992) compared the growth rates of individuals classified as dominant and subdominant, and a third class ("floaters") of fish that were not associated with dominance hierarchies. The growth rate of coho salmon that left the study sections was unknown, so it would be inappropriate to compare the movers in our study with the "floaters" in Nielsen's (1992) study.

Comparison of the physical habitat features and level of competition in units where fish stayed and where they departed yielded important results. Coho salmon movement seemed to be motivated primarily by habitat size and especially depth. This is consistent with the preference of the species for pools (e.g., Bisson et al. 1988), with experimental evidence that probability of mortality was related to habitat complexity and depth when area was controlled for (Lonzarich and Quinn 1995), and with higher mortality rates in riffles than in pools (Kruzic et al. 2001). Depth may confer greater protection from avian predation than area, though deep pools may also be more suitable for predatory fishes such as larger salmonids (although few trout greater than age-1+ were observed).

The habitat units that coho left actually had lower densities than the units where they remained, in contrast with the assumption that movement takes place as a result of competition for space. Combined with the evidence that the coho that moved were similar in size to those that remained, this indicates that movement was more a matter of habitat selection than displacement. It seems that coho salmon in high-quality habitats (in our case deep, but other attributes may also be important) tend to remain there despite comparatively high densities. Indeed, the higher density may be a consequence of reluctance to leave. These habitats may afford protection at the expense of growing conditions, as growth is density dependent (e.g., Roni and Quinn 2001). Fish in small, shallow habitats tend to leave despite the fact that (or resulting in the fact that) densities in such habitats are low. Fish in small, shallow habitats may be the first to experience the inadequacies of their habitats as their body size increases, and this would be especially true of the fastest-growing fish in the smallest, shallowest habitats. Such movement by fish that outgrew their habitat was reported by Forseth et al. (1999) for older juvenile brown trout (*Salmo trutta*). Fish that moved encountered suitable habitat and grew faster than individuals that remained. However, it remains unclear whether the faster growth rates of movers were attributable to some superiority of the habitat to which they moved, or to an inherently faster growth rate possessed by those fish. The lack of significant differences in the initial lengths of movers and nonmovers suggests that movers encountered superior foraging opportunities.

Stream characteristics and movement

Both upstream and downstream distances moved (in terms of habitat units) were similar in all streams except Griffin Creek, where coho salmon moved farther downstream and shorter distances upstream than in the other streams. Shuwah Creek and BBC are both forced pool-riffle channels with gradients of 2% or less, whereas Griffin Creek is a relatively high-gradient (5.7%) step-pool/cascade channel. Thus, extensive upstream movement in Griffin Creek would have been more difficult than in BBC or Shuwah Creek. A more extensive study design, including a range of gradients, would be needed to test the hypothesis that juvenile coho salmon movements are affected by gradient per se. However, the step-pool and cascade channel types characteristic of higher gradients are less extensively used by coho salmon than the

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pool-riffle and plane bed channels found at lower gradients (Montgomery et al. 1999), making such a comparative study difficult.

Unlike the other streams, the number of downstream movement events by coho salmon exceeded upstream movement events in Griffin Creek. Several hundred meters of Griffin Creek upstream of the study section went dry by the 10 August 1998 snorkel survey, precluding further upstream movement. Fish may have moved downstream to avoid dewatering, as Hubble (1992) noted for age-0+ steelhead in intermittent tributaries to Satus Creek, Wash. Dewatering also occurred in Shuwah Creek but started from the downstream end, and only affected the lower sixth of the study section.

Both Griffin and Shuwah Creeks have similar bankfull widths and discharges, and portions of each became intermittent. These similarities in flow regime probably explain the greater proportions of salmonids moving in these streams than in BBC, despite the differences in channel type and gradient. The rapid loss of suitable habitat in Shuwah and Griffin Creeks as flow declined resulted in increased fish mobility. The flow in Griffin Creek declined earlier and more drastically than in Shuwah Creek and even more fish moved in Griffin Creek than in Shuwah Creek.

Downstream movement may have additional adaptive significance (beyond the avoidance of dewatered sections) in the east fork of Griffin Creek because of the distribution of high-quality rearing habitat in the Griffin Creek system. The majority of high-quality rearing habitat for coho salmon occurs downstream from the study section on East Fork Griffin Creek, in the form of large in-channel wetlands on the main stem of Griffin Creek. Quinn and Peterson (1996) reported increased overwinter survival and larger smolt size by coho salmon rearing in headwater wetlands on BBC. Perhaps downstream movement produces similar advantages for coho in Griffin Creek as well.

In conclusion, we observed that small-scale movement (i.e., several habitat units) and especially upstream movement was common in three streams. The direction of movement was influenced by channel type and (or) gradient (steeper-gradient step-pool channels being associated with more frequent and greater movement downstream). However, sampling of additional reaches and streams with a wider range of gradients and channel types is needed to test the relationship between movement direction and channel type and (or) gradient, and rule out the influence of habitat dewatering. Our results were consistent with the hypothesis that habitat quality rather than social dominance was the primary factor affecting movement by coho salmon in our study streams, and that movers were neither initially inferior to those that remained nor were they less likely to thrive. This is an important perspective on the behavioral ecology of juvenile anadromous salmonids, and also has implications for the design and interpretation of studies on habitat quality, restoration, and salmonid populations as well as the management of those populations. For example, stream road-crossings and smolt counting fences should be designed to accommodate the upstream movements of juvenile anadromous salmonids and movement studies should be designed to detect movements at multiple spatial and temporal scales. Finally, substantial portions of the habitat in the study streams dewatered, which is likely an important factor in the ecology of movement in streams that are regularly or occasionally intermittent. If late summer dewatering occurs regularly, then the propensity to move in the summer would be an advantage. Thus, declining discharge may be both a proximate stimulus and an evolutionary pressure affecting salmonid movement.

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