Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools

Bret C. Harvey

Abstract: Over 4 months and about 1 year, coastal cutthroat trout *(Oncorhynchus clarki clarki)* ≥ age-1 in Little Jones Creek, California, remained at similar rates in pools with and without large woody debris. This result was based on attempts in July and November 1995 to collect and tag all fish in 22 pools and three collections of fish from the same pools in November 1995, May 1996, and August 1996. Retention of fish appeared to be greater in pools with large woody debris in May 1996. The presence of large woody debris in pools did not influence immigration or growth of cutthroat trout. However, both immigration and growth increased downstream over the 3850-m study reach. Low retention and substantial immigration of cutthroat trout into experimental pools indicate that movement is important in the dynamics of this population. First- and second-order channels appear to be important sources of fish for the third-order study reach, while the study reach may export significant numbers of fish to downstream reaches accessible to anadromous fish.

Résumé : Pendant des périodes de 4 mois et dun an environ, des truites fardées côtières *(Oncorhynchus clarki clarki)* du ruisseau Little Jones (Californie) âgées ≥ 1 an sont demeurées, à des taux semblables, dans des tosses où de gros débris ligneux étaient présents on non. Ces résultats ont été obtenus suite a des tentatives faites en juillet et novembre 1995 de prélever et de marquer tous les poissons se trouvant dans 22 fosses, et à trois prelévèments de poissons dans ces mêmes fosses faits en novembre 1995, mai 1996 et août 1996. Il semble que les poissons soient plus demeurés dans les tosses où les débris ligneux étaient gros en mai 1996. La présence de gros débris ligneux n'a pas influé sur 1'immigration on la croissance des truites fardées. Par ailleurs, tant 1'immigration que la croissance augmentaient vers 1'aval, sur les 3850 mètres du segment de cours d'eau étudié. Une faible reténtion et une immigration appréciable des truites fardées dans des tosses expérimentales indiquent que le déplacement joue un rô1e important dans la dynamique de cette population. Les chenaux d'ordres 1 et 2 semblaient être d'importantes sources de poissons pour le segment étudié, d'ordre 3, et ce dernier pouvait exporter des nombres appréciables de poissons vers Faval, accessible aux poissons anadromes.

[Traduit par la Rédaction]

Introduction

Quantifying the quality of different habitats for species and communities is one of the fundamental challenges in ecology and a basic need of natural resource managers. Often, habitat-specific densities of animals are used as measures of habitat quality, but correlation between density and the value of habitats to animal populations may not always exist (Van Horne 1983). Ideally, assessment of the value of habitats would include measurement of habitat-specific survival and reproduction by individuals, but such information can be difficult to obtain, particularly where animals normally utilize multiple habitats. In these situations, information on movement and growth may be relevant to the assessment of habitat quality. Winker et al. (1995) proposed recently that for some territorial organisms, movement rates within habitats could provide an index of habitat quality. These authors predicted that turnover would be relatively low in superior habitat where dominant individuals defend territories, while poor environmental conditions in lower quality habitat could contribute to relatively high turnover there. Growth may relate to habitat quality in that individuals who dominate the highest quality habitats should have relatively high growth rates.

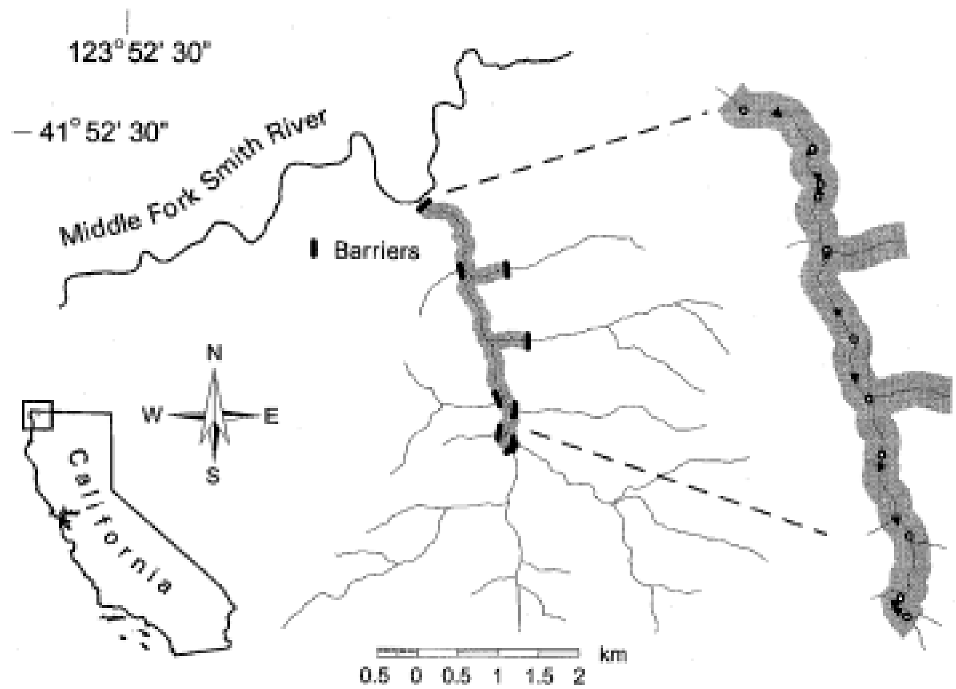
The idea that differences in movement can reflect the value of habitats for stream fishes is supported by observations that instream habitat enhancement in six Colorado streams increased trout density mainly through immigration (Gowan and Fausch 1996a). The movement of individuals, including adults, can play an important role in the population dynamics of salmonids in streams (e.g., Gowan et al. 1994; Gowan and Fausch 1996b; Northcote 1997).

The value of large woody debris and other large substrate elements as components of habitat for fish in streams has been often investigated. Formation of pools by large substrate elements can benefit some fish populations (e.g.,

Received November 5, 1997. Accepted April 30, 1998.
J14286

B.C. Harvey. USDA Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, U.S.A.
e-mail: bch@axe.humboldt.edu

Fig. 1. Little Jones Creek, Del Norte County, California, with the study area shaded. Dark bars represent barriers to upstream movement by fish. In the enlargement at right, open circles indicate simple pools and solid triangles indicate complex pools. Simple pools contained no cover for fish, while complex pools contained large woody debris and other large substrate elements.



Fausch and Northcote 1992), but the value of the presence of large substrate elements per se is less clear. Woody debris can provide refuge from high discharge for fish (e.g., McMahon and Hartman 1989) but may also reduce foraging success (Wilzbach et al. 1986). In Little Jones Creek, northwestern California, the density of cutthroat trout in pools is not strongly related to the amount of woody debris (B.C. Harvey and J.A. Simondet, unpublished data). However, differences in habitat quality between the two types of pools might be reflected by parameters other than density. In this study, I tested the null hypotheses that retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) do not differ in pools with and without large woody debris. The experimental design also allowed evaluation of longitudinal patterns in movement and growth in a population of "resident" cutthroat trout.

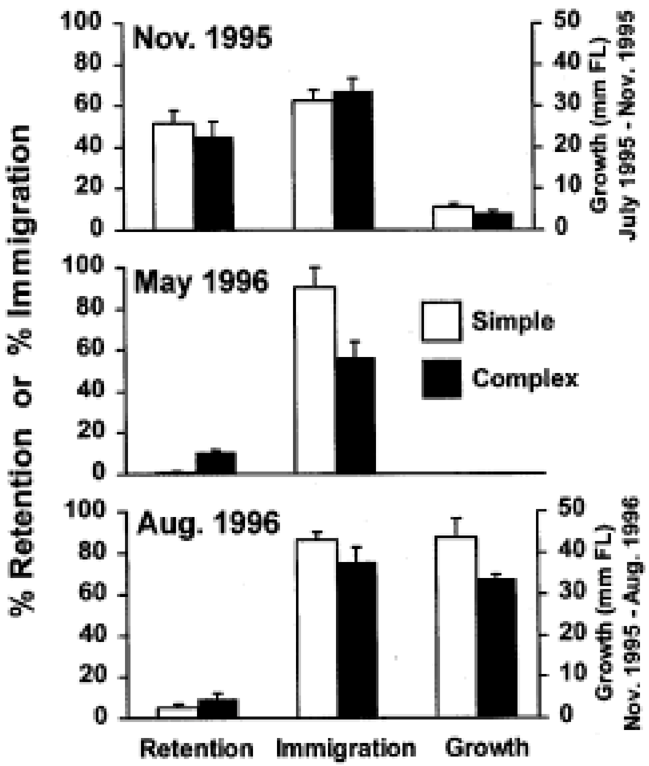
Study site and methods

Little Jones Creek is a third-order tributary of the Middle Fork Smith River in northwestern California. Elevation ranges from 268 m at the mouth to 354 m at the upstream end of the study reach, while the maximum elevation of terrain within the watershed is about 1100 m. About 30% of the 2750-ha watershed has been logged in the last 50 years. The watershed has steep slopes with an overstory of Douglas-fir *(Pseudotsuga menziesii)* and tan oak *(Lithocarpus densiflora)*. A high density of red alder *(Alnus rubra)* provides a nearly complete riparian canopy throughout the study reach. The drainage receives most precipitation as rain from October to April. Average annual precipitation exceeds 335 cm. Summer baseflow of the creek is about 0.15 $m^3 s^{-1}$, while winter storms produce discharges >30 $m^3 s^{-1}$. Stream gradient is 2.2% over the study reach, which extends 3850 m from a 6-m-high waterfall 50 m from the confluence of Little Jones Creek and the Middle Fork Smith River upstream to the confluence of Little Jones Creek and a tributary of about equal size (Fig. 1). Barriers to upstream movement by fish are present on both channels at the upper end of the study reach. There are no barriers to fish movement within the study reach, where coastal cutthroat trout is the only fish species. Cutthroat trout occur above the barriers in the two streams at the upper end of the study reach and above barriers in two tributaries entering Little Jones Creek within the study reach. Fish density in these upstream areas has not been quantified, but electrofishing and direct observations by divers have revealed that cutthroat trout are common in pools above the barriers in all four streams.

Large cutthroat trout in the study reach are concentrated in pools. For 171 observations of habitat-specific fish density made over 3 years, cutthroat trout > age-1 were about three times more abundant in pools compared with fast-water habitats (B.C. Harvey and J.A. Simondet, unpublished data). Pools formed by scour around logs and rootwads contained more cutthroat trout ≥ age-1 (0.25 fish m^{-1} for 18 observations over 3 years) than pools formed by scour around bedrock (0.16 fish m^{-1} for 31 observations). However, this difference is not strong whether analyzed by pooling data across years (*t*-test: $P = 0.12$) or by incorporating variation among years by expressing density within habitats as an index (Bisson et al. 1988) based on mean density within years ($P = 0.08$).

To contrast retention, immigration, and growth of cutthroat trout in pools without large substrate elements (hereafter referred to as "simple" pools) and those containing large woody debris ("complex" pools), while attempting to control for any longitudinal effects on the response variables, I used as experimental units 11 pairs of pools (one simple and one complex) distributed throughout the study reach. The longitudinal positions of pools ranged 225-3850 m from the mouth of Little Jones Creek. The two pools in each simple/complex pair were separated by an average of 85 m (SE = 19 m). The 22 experimental pools comprised about 40% of all pools in the study reach. Simple pools were formed by lateral scour adjacent to bedrock and contained no woody debris,

Fig. 2. Retention, immigration, and growth of cutthroat trout in simple and complex pools in Little Jones Creek, California. November 1995 data are based on 308 fish tagged in July 1995. May and August 1996 data are based on 507 fish tagged in July and November 1995. For both pool types, means are based on observations of 11 pools, with the exception of growth in complex pools in November 1995 (*n* = 10), immigration into simple pools in May 1996 (*n* = 5), and growth in August 1996 (*n* = 6 for both pool types).



undercut banks, or unembedded cobbles and boulders. Nine of the complex pools were formed by scour around large woody debris, while the other two were formed by scour adjacent to bedrock. With one exception, complex pools all contained exposed roots and woody debris that provided extensive cover for fish. The exception contained large woody debris and >2 m^2 of space beneath large boulders, much of it 40-60 mm in height. This boulder habitat is appropriate for fish concealing themselves in the substrate (Gregory and Griffith 1996). Pools included in the experiment were identified with metal tags attached to trees at the streambank. The study reach was flagged every 25 m to help locate fish recaptured outside the pools where they were tagged.

To begin the experiment, fish in all experimental pools were collected on 20, 21, and 28 July 1995 by multiple-pass electrofishing. The field crew made at least three electrofishing passes in each pool. No more than one fish was collected on the final pass in any pool. Collecting stopped when a snorkeler located fewer than two fish ≥ 85 mm fork length (FL), assumed to be ≥ age-1, in a pool. After electrofishing, no fish other than age-0 were apparent in 18 of the 22 experimental pools. The effectiveness of multiple-pass electrofishing in collecting fish from these pools is indicated by a previous recolonization experiment in Little Jones Creek in which cutthroat trout ≥ age-1 were removed from nine pools. One day after electrofishing, the density of ≥age-1 fish in all pools was <7% of densities before removal (B.C. Harvey, unpublished data). In this study, all fish ≥ age-1 collected from experimental pools (308 fish in July) received a passive integrated transponder (PIT) tag by injection into the body cavity. These tags allow identification of individual fish using a hand-held scanner. A preliminary laboratory study revealed no effects of the tags on survival and growth over 21 days, and growth of tagged fish during the study equaled that of unmarked fish as indicated by the size-frequency distribution of the latter. Finally, tagged fish were measured to the nearest millimetre FL and released into the pool where they were captured.

A field crew electrofished the experimental pools again on 10-12 November 1995. Electrofishing in November was conducted at night because snorkelers observed many more fish at night compared with day before this collecting effort and previous experience revealed higher capture rates at night under these conditions. Concealment during the day and exposure at night by salmonids has been widely observed during winter and in cold temperatures at other times of the year (Heggenes et al. 1993; Fraser et al. 1995). Headlamps and a 500-W halogen lamp powered by a backpack-mounted generator aided nighttime collecting. Again, no more than one fish >_ age-1 was collected on the final pass in any pool and a snorkeler assessed electrofishing success in each pool. No more than one >_ age-1 fish was observed in any experimental pool after electrofishing. All but age-0 fish collected in experimental pools were checked for PIT tags and all fish collected were measured (FL). In nine of the 11 pairs of pools, all ≥ age-1 cutthroat trout collected that did not have PIT tags implanted in July received them in November (199 fish). A shortage of tags prevented tagging of 55 fish captured in two pairs of pools (at longitudinal positions 835 and 855 m and 1890 and 2070 m). Also in November, the field crew conducted one-pass electrofishing throughout the study reach and all individuals ≥ age-1 were checked for PIT tags.

From 10 to 12 May and from 5 to 6 August 1996, fish were again collected from experimental pools (during the day) by multiple-pass electrofishing and from the remainder of the study reach by one-pass electrofishing. On these dates, all fish were scanned for PIT tags and measured; no additional PIT tags were implanted. Also in 1996, the field crews sampled two first-order tributaries that enter Little Jones Creek within the study reach. The two tributaries were sampled upstream from Little Jones Creek to apparent barriers to upstream movement by fish.

To incorporate any longitudinal effects on retention of tagged fish and immigration by untagged fish, I contrasted these response variables in simple and complex pools using paired *t*-tests. Retention of tagged fish was calculated for November 1995 and the two collections in 1996 and was defined as the proportion of fish previously tagged in a given pool that were subsequently recovered in the same pool. For the May and August 1996 collections, fish tagged in both July and November 1995 were included in the calculations.

Immigration was also quantified for the three collecting efforts following the initial tagging and was defined as the proportion of fish in a given pool not tagged but large enough to have been tagged previously (following Gowan and Fausch 1996*a*). For each of the three resampling efforts, untagged fish greater than or equal in size to the smallest tagged fish collected were included in the estimates of immigration.

I also compared fish growth (millimetres FL) in simple and complex pools using paired *t*-tests. Only fish recovered in the same pool from which they were first collected were included in the analysis of the November data, which was based on pool-specific means. For 1996 collections, only fish that were recovered in the same pool each time they were collected were included in the analyses of fish growth by pool type. Most fish included in the August 1996 contrast of growth in simple and complex pools were tagged or recaptured in November 1995; thus, their lengths in November 1995 provided the initial FL for quantifying individual growth. For fish tagged in July 1995 and collected in August 1996 but not in

Fig. 3. Immigration by fish into pools of Little Jones Creek, California, expressed as the percentage of fish that had not been tagged during intensive collecting from the pools in July 1995 for the November 1995 data and in July and November 1995 for the May and August 1996 collections. May 1996 data include only results for pools with large woody debris because few fish were captured from simple pools. Longitudinal position refers to the distance upstream from the confluence of Little Jones Creek and the Middle Fork Smith River.

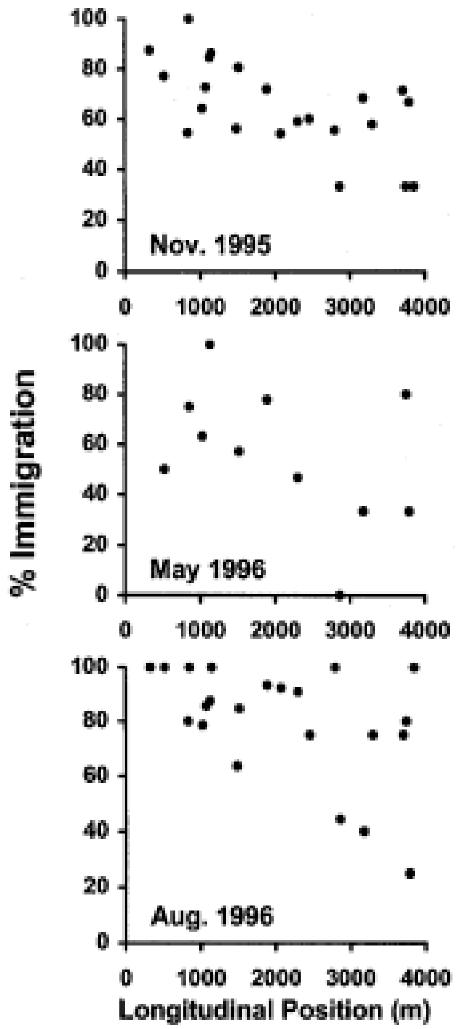
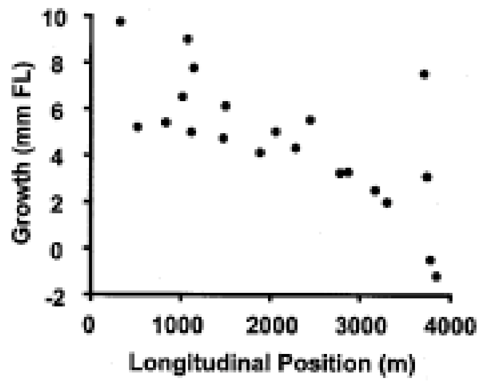


Fig. 4. Average growth by cutthroat trout ≥ age-1 in 21 pools in Little Jones Creek, California, from July to November 1995. Pool-specific values are based on an average of seven fish. The datum at longitudinal position = 3710 m, growth = 7.5 mm is based on the smallest sample size in the data set, two fish. Longitudinal position refers to the distance upstream from the confluence of Little Jones Creek and the Middle Fork Smith River.



November 1995, I estimated size in November 1995 based on the growth rate of fish tagged in July 1995 and recaptured in November 1995. I then used that estimated size in November 1995 as the initial size for computing growth to produce estimates comparable with those for fish captured in both November 1995 .and August 1996. I did not attempt to contrast growth by fish from simple and complex pools in May 1996 because of low sample size for simple pools.

Results

In November 1995, tagged cutthroat trout were recovered from the habitats they occupied in July 1995 at similar rates in simple and complex pools (Fig. 2; paired *t*-test: n = 11, P = 0.512). From all 11 simple pools, the field crew recovered 66 of 132 fish tagged in July, while the 11 complex pools yielded 84 of 176 fish tagged previously. Only 13 fish were captured outside the pools where they were tagged in July. The total recovery rates of tagged fish from throughout the study reach in November were similar for fish captured in simple and complex pools in July (simple: 75 of 132 (56.8%); complex: 88 of 176 (50%)). Low discharge in November 1995 compared with July 1995 probably led to higher capture efficiency in November.

More ≥ age-1 fish were captured in experimental pools in November 1995 than in July 1995 and immigration of untagged fish into simple and complex pools was similar (Fig. 2; paired *t*-test: n = *11*, P = *0*.555). Fish growth was marginally higher in simple than in complex pools (Fig. 2; paired *t*-test; n = 10, P = 0.077). I excluded one pair of pools from the November analysis of growth because no tagged fish were recovered from the complex pool in that pair. Growth (millimetres FL) and the initial size of tagged cutthroat trout were not related in this (n = 163, r^2 < 0.001) or subsequent collections.

In May 1996, the entire study reach yielded only 47 of 507 fish tagged in July and November 1995, but 31 of these were collected in the complex pools where they were tagged. Retention of tagged fish appeared to be greater in complex pools (one of 218 fish tagged in simple pools, 31 of 289 (10.7%) fish tagged in complex pools; paired *t*-test: n = 10, P < 0.001). High stream flow prevented access to the most downstream pool in May. Almost all tagged fish collected throughout the study reach in May 1996 were captured in habitats containing woody debris. Five of the seven fish tagged in simple pools in 1995 and recovered in May 1996 occupied complex habitats when captured in May, but none occupied the complex pool adjacent to the simple pool where they were tagged. All 40 fish tagged in complex pools in 1995 and recovered in May 1996 were captured either in complex habitats in the main channel or in first-order tributaries. However, while observations by snorkelers 1 week before the May collecting effort revealed cutthroat trout in the water column during the day in both simple and complex pools, fish apparently did not occupy the water column in simple pools during this sampling. Nighttime sampling

Table 1. Comparison of upstream and downstream movement by tagged cutthroat trout recaptured outside the pools where they were tagged in a 3850-m reach of Little Jones Creek, California.

	Nov. 1995	May 1996	Aug. 1996
No. recovered upstream	8	8	14
Mean distance moved (m)	178	510	100
Maximum distance moved (m)	1000	1970	490
No. recovered downstream	5	7	12
Mean distance moved (m)	138	323	284
Maximum distance moved (m)	555	1030	1525

Note: November results are based on 308 fish tagged in July 1995, while May and August 1996 results include data on an additional 199 fish tagged in November 1995. Distances moved are based on the locations where fish were first captured and tagged.

would probably have yielded greater numbers of fish in both simple and complex pools. High stream discharge also probably contributed to low capture rates in May.

Contrasting immigration into simple and complex pools is problematic for May 1996 because no fish were captured in five of the 10 simple pools sampled. For the pairs of pools that include the five simple pools where fish were captured, immigration was not different in the two types of pools (paired *t*-test: $n = 5$, $P = 0.283$). Immigration ranged from 0 to 100% in complex pools and averaged 56%. Immigration was 100% in four simple pools based on the capture of one untagged fish in each and 50% in one pool where one tagged fish and one untagged fish were captured. Growth in simple and complex pools could not be compared because only one tagged fish was captured from a simple pool.

Low retention of tagged fish was also evident in August 1996, but retention was similar in simple and complex pools (Fig. 2; paired *t*-test: $n = 11$, $P = 0.321$). Only 11 of 218 (5.0%) fish tagged in simple pools and 20 of 289 (6.9%) fish tagged in complex pools were found in the pool where they were first captured. Overall, 24 fish (11.0%) tagged in simple pools and 30 fish (10.4%) tagged in complex pools were recaptured in August 1996. Immigration was also similar in simple and complex pools in August (Fig. 2; paired *t*-test: $n = 11$, $P = 0.269$).

Low retention of tagged fish led to a relatively weak contrast of fish growth in simple and complex pools for August 1996. Tagged fish that were never captured other than in the pool where they were first collected were recovered from both pools in six simple/complex pairs in August 1996. Average growth of these fish in the experimental pools revealed no difference between pool types (Fig. 2; paired *t*-test: $n = 6$, $P = 0.14$).

The longitudinal position of the experimental units influenced immigration and fish growth on one or more collecting dates, but never influenced retention of tagged fish. For both November 1995 and August 1996, immigration into the 22 experimental units declined with distance upstream (Fig. 3; for November 1995: $r^2 = 0.39$, $P = 0.002$; for August 1996: $r^2 = 0.23$, $P = 0.024$). For May 1996, excluding data from simple pools where at most two fish were captured, immigration was not related significantly to longitudinal position (Fig. 3; $n = 11$, $r^2 = 0.18$, $P = 0.196$).

Growth of cutthroat trout between July and November 1995 averaged only 5 mm ($n = 163$) and declined with distance upstream. The pool-specific average growth for fish collected in November 1995 from the pools where they were tagged in July 1995 was negatively related to the longitudinal position of the pools (Fig. 4; $n = 21$, $r^2 = 0.51$, $P < 0.001$). Predictably, the relationship is weaker but also highly significant based on the growth of individual tagged fish caught in the same pool in both July and November ($n = 150$, $r^2 = 0.22$, $P < 0.001$).

Growth also was related to longitudinal position between November 1995 and May 1996 and averaged 15 mm for all fish captured in both months. For fish caught in the same pool in both months, growth was negatively related to longitudinal position ($n = 26$, $r^2 = 0.19$, $P = 0.029$).

The data set provides little information about longitudinal patterns in growth between May and August 1996 because only 11 individuals were captured in both months and only seven of these were captured in the same pool. Growth for the interval averaged 18 mm, but was unrelated to longitudinal position ($P > 0.10$).

Recovery of tagged fish throughout the study reach indicated highly variable movement among individuals. Some tagged fish appeared to have home ranges limited to one channel geomorphic unit: 26 of 54 tagged fish captured in August 1996 were collected from the same pool every time they were caught. However, substantial movement by some tagged individuals was apparent between all sampling dates (Table 1). Individual movements were greatest between November 1995 and May 1996 (Table 1), when the field crew recovered tagged fish in first-order tributaries and up to 1970 m upstream of their original positions in Little Jones Creek. The numbers of fish captured upstream versus downstream of their previous location were similar for all three collections (Table 1).

Discussion

Retention and immigration rates of cutthroat trout in Little Jones Creek together suggest high rates of movement by fish in this system. Young (1996) also observed high rates of movement by cutthroat trout in a study of Colorado River cutthroat trout *(Oncorhynchus clarki pleuriticus)* using radiotelemetry. While earlier studies that have quantified movement by repeated collection of tagged fish have suggested spatial stability in cutthroat trout populations (Miller 1957; Heggenes et al. 1991), the design of these studies focused on the locations of tagged fish that were recovered and did not examine immigration of untagged fish into stream sections where a high proportion of fish were tagged initially (Gowan et al. 1994). Studies taking the latter approach have concluded that movement is common in populations of stream salmonids (Smith and Saunders 1958; Cunjak and Randall 1993; Riley and Fausch 1995; Gowan and Fausch 1996b). The low recapture rate in this study is not unusual: in 14 of the 33 studies of movement by salmonids in streams reviewed by Gowan et al. (1994), ≥75% of tagged individuals were not recaptured. One weakness of this and many previous studies is the inability to distinguish mortality and emigration. However, the hypothesis that some cutthroat trout in Little Jones Creek are highly mobile is supported by the fact that nine pools from which all cutthroat trout were removed regained their original number and size distribution of fish in about 5 weeks during summer 1993 (B.C. Harvey, unpublished data).

The capture of few tagged fish outside the experimental units appears to conflict with the high level of movement suggested by retention and immigration rates in experimental pools. However, sampling effort outside the experimental units was relatively low in this study. Also, Gowan and Fausch (1996*a*) measured high rates of immigration by salmonids into 500-m-long study reaches in six Rocky Mountain streams, implying that long-distance movements by salmonids may be common. At least 8.5 km of channel upstream of, and tributary to, the study reach (Fig. 1) contained cutthroat trout and thus could have provided immigrants to the experimental pools. Long downstream movements by fish in the study reach would place them in the Middle Fork Smith River. The pattern of increasing immigration downstream is consistent with the hypothesis that fish emigrate from the study reach into the Middle Fork Smith River. Age-1 cutthroat trout have been captured in the spring with a fyke net at the base of the falls at the downstream end of the study reach (B.C. Harvey and J.A. Simondet, unpublished data).

The increase in growth rate downstream may influence movement patterns by cutthroat trout in Little Jones Creek, with the caveat that growth was estimated on the basis of fish that remained stationary and thus may not reflect the experience of mobile fish. Wilzbach's (1985) observation that cutthroat trout emigrated more readily from artificial channels with relatively low food supply supports a connection between movement and growth rate. However, in isolated populations above barriers to upstream passage, mechanisms that might promote downstream movement would be opposed by selection to remain in place.

Previous researchers have observed faster growth downstream by stream fishes (Anderson 1985; Greenberg and Brothers 1991), but perhaps never over a distance of only 4 km. A longitudinal gradient in temperature, with consequences for both the bioenergetics of the fish (Brett et al. 1969) and secondary production (Morin and Dumont 1994), may influence this pattern in growth. However, the extensive alder canopy and small change in elevation in the study reach suggest minor longitudinal differences in water temperature.

The presence of large woody debris within pools in Little Jones Creek appears to have no effect on cutthroat trout movement or growth during some parts of the year. Several factors may contribute to this result: (*i*) when discharge is low or moderate, water depth and surface turbulence in simple pools may provide adequate cover for fish, (*ii*) food availability may be the dominant factor controlling habitat selection by cutthroat trout and may be unrelated to the presence of woody debris, (*iii*) any benefit from the presence of large woody debris may be offset by the advantage of increased foraging efficiency in simple habitats (Wilzbach et al. 1986), a hypothesis supported by the trend toward faster growth in simple pools observed in this study, and (*iv*) fish may commonly use habitat on a spatial scale larger than individual channel geomorphic units. Thus, fish captured in simple pools may benefit from habitat complexity in nearby areas.

While results for May 1996 appear to provide evidence for higher retention of fish in complex pools during relatively high stream flow and low water temperature, sampling issues affect the interpretation of these data. Direct observations from a previous experiment in Little Jones Creek revealed significantly more fish exposed in both simple and complex pools at night compared with day in winter but similar numbers during night and day in summer (B.C. Harvey and J.A. Simondet, unpublished data). Observations of radiotagged cutthroat trout in Little Jones Creek during winter showed that some fish move into simple pools at night but occupy adjacent riffles during the day, while others occupy complex pools continuously (B.C. Harvey, unpublished data). Although observations 1 week prior to the May 1996 daytime sampling effort revealed no significant differences in numbers of fish exposed during the day versus at night in simple or complex pools, short-term changes in daytime concealment characterize the behavior of salmonids (Heggenes et al. 1993; Fraser et al. 1995). Nighttime sampling in May would probably have yielded more fish from both simple and complex pools than were captured during the day.

This study has several implications for resource managers. High rates of immigration into experimental pools in a reach where access from downstream was blocked and use by cutthroat trout from third-order Little Jones Creek of first-order tributaries in May suggest that first- and second-order streams can be important in the large-scale population dynamics of cutthroat trout. Also, the apparent export of fish over a barrier to upstream migration at the mouth of Little Jones Creek indicates that resident subpopulations may need to be considered as sources of individuals for populations with anadromous components. This study supports the suggestion by Gowan et al. (1994) for Rocky Mountain streams that high rates of movement by trout, apparently often over long distances, imply that management of these fish must involve analysis of habitat and populations over large spatial scales.

Acknowledgements

I greatly appreciate the assistance in the field provided by Eric Eichlin, Tim Hayden, Baker Holden, Mike McCain, Rod Nakamoto, Aaron Pittman, Gary Reedy, Scott Riley, James Robertson, Margaret Sargent, Hans Voight, and particularly Jim Simondet and Jason White. The manuscript was improved by the comments of Tom Lisle, Hart Welsh, and Mike Young.

References

Anderson, C.S. 1985. The structure of sculpin populations along a stream size gradient. Environ. Biol. Fishes, **13**: 93-102.

Bisson, PA., Sullivan, K., and Nielsen, J.L. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. **117**: 262-273.

Brett, J.R., Shelbourn, J.E., and Shoop, C.T. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. **26**: 2363-2394.

Cunjak, R.A., and Randall, R.G. 1993. Instream movements of young Atlantic salmon during winter and early spring. In Production of juvenile salmon, *Salmo salar*, in natural waters. Edited by R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 43-51.

Fausch, K.D., and Northcote, T.G. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Can. J. Fish. Aquat. Sci. **49**: 682-693.

Fraser, N.H.C., Heggenes, J., Metcalfe, N.B., and Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Can. J. Zool. **73**: 446-451.

Gowan, C., and Fausch, K.D. 1996*a*. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecol. Appl. **6**: 931-946.

Gowan, C., and Fausch, K.D. 1996*b*. Mobile brook trout in two high-elevation Colorado streams: reevaluating the concept of restricted movement. Can. J. Fish. Aquat. Sci. **53**: 1370-1381.

Gowan, C., Young, M.K., Fausch, K.D., and Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. **51**: 2626-2637.

Greenberg, L.A., and Brothers, E.B. 1991. Intrastream variation in growth rates and time of first otolith increment formation for young of the year *Etheostoma simoterum* (Cope) (Perciformes: Percidae). J. Fish Biol. **38**: 237-242.

Gregory, J.S., and Griffith, J.S. 1996. Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions. Can. J. Zool. **74**: 451-455.

Heggenes, J., Northcote, T.G., and Peter, A. 1991. Spatial stability of cutthroat trout (Oncorhynchus clarki) in a small, coastal stream. Can. J. Fish. Aquat. Sci. **48**: 757-762.

Heggenes, J., Krog, O.M., Lindas, OR., Dokk, J.G., and Bremnes, T. 1993. Homeostatic behavioural responses in a changing environment: brown trout (Salmo trutta) become nocturnal during winter. J. Anim. Ecol. **62**: 295-308.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon. Can. J. Fish. Aquat. Sci. **46**: 1551-1557.

Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. J. Fish. Res. Board Can. 14: 687-691.

Morin, A., and Dumont, P.A. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. J. N. Am. Benthol. Soc. **13**: 357-367.

Northcote, T.G. 1997. Potamodromy in salmonidae - living and moving in the fast lane. N. Am. J. Fish. Manage. **17**: 1029-1045.

Riley, S.C., and Fausch, K.D. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Can. J. Fish. Aquat. Sci. **52**: 34-53.

Smith, M.W., and Saunders, J.W. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. J. Fish. Res. Board Can. **15**: 1403-1449.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. **47**: 893-901.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Can. J. Fish. Aquat. Sci. **42**: 1668-1672.

Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology, **67**: 898-911.

Winker, K., Rappole, J.H., and Ramos, M.A. 1995. The use of movement data as an assay of habitat quality. Oecologia, **101**: 211-216.

Young, M.K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Can. J. Fish. Aquat. Sci. **53**: 1403-1408.