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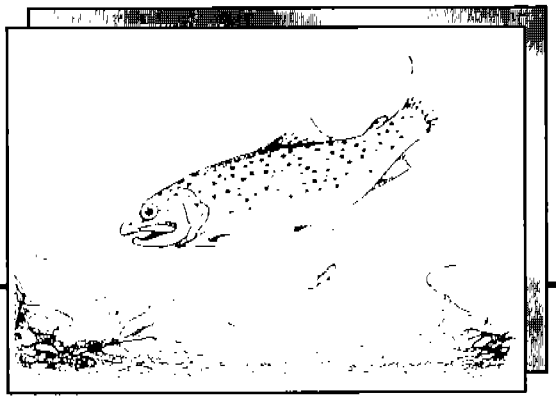

Resident Trout and Movement: Consequences of a New Paradigm

Michael K. Young

Rocky Mountain Forest and Range Experiment Station
222 S. 22nd Street,
Laramie, Wyoming 82070

Abstract

Trout living in streams have been thought to move very little throughout their entire lives. Recent research has demonstrated that adult brown trout, Colorado River cutthroat trout, brook trout, and rainbow trout were far more mobile than previously believed. The mobility of trout has probably affected estimates of fish abundance, perceptions of habitat quality, and the delineation of populations, and could nullify the desired outcome of restrictive angling regulations. Also, by fragmenting streams we may be reducing the probability of persistence of native trout populations by restricting movement and thus restricting population size.

Restricted Movement: The Prevailing Paradigm

Unlike their anadromous relatives, stream-resident trout are often considered to be relatively immobile. For example, Northcote (1992) stated that the "home ranges for [such] yearling and older salmonids are ... usually a few tens of meters." The notion of restricted movement of stream-dwelling trout has persisted for over 50 years (Hoover and Johnson 1937; Gerking 1959), and has been applied to trout species as different as cutthroat trout *(Oncorhynchus clarki)* (Miller 1957; Heggenes et al. 1991) and brown trout *(Salmo trutta)* (Stefanich 1952; Bachman 1984).

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The USDA Forest Service Fish Habitat Relationships Program was established to further the development of fisheries technology and transfer this technology to field biologists. With ever increasing demands for natural resources, protection and management of aquatic communities requires biologists to be knowledgable of current research findings and state-of-the-art techniques. The purpose of *FHR Currents* is to provide a vehicle to quickly disseminate information important to field-level biologists in the USDA Forest Service.

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If you wish to submit a paper for publication in *FHR Currents*, please contact the following people for information and guidelines:

Jerry Boberg/Karen Kenfield
Technical Editors
(707) 441-3669

Six Rivers National Forest
Fisheries Department
1330 Bayshore Way
Eureka, CA 95501

Art work by:
Jerry Boberg,
Six Rivers National Forest

Forest Service Fish Habitat Relationships Program Leaders or Representatives

National FHR Program

Jeffrey L. Kershner
Washington Office
Fish & Wildlife Department
Utah State University
Logan, UT 84322-5210

Region 1

Kathy Moynan, Northern Region
(Anadromous Fish Program)
Nez Perce National Forest
Route 2, Box 475
Grangeville, ID 83530

Brian Sanborn, Northern Region
(Resident Fish Program)
Deerlodge National Forest
Federal Building, Box 400
Butte, MT 59703

Region 2

R. Nick Schmal, Rocky Mountain Region
Wildlife, Fish & Botany Staff
Univ. of Wyoming, College of Agriculture
P.O. Box 3354
Laramie, WY 82071-3354

Region 3

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Wildlife, Fish & Botany Staff
Federal Building
517 Gold Avel, S.W.
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Region 4

Seona L. Brown, Intermountain Region
Wildlife, Fish & Botany Staff
324 25th St.
Ogden, UT 84401

Region 5

Jerry Boberg, Pacific Southwest Region
(Anadromous Fish Program)
Six Rivers National Forest
1330 Bayshore Way
Eureka, CA 95501

Jeffery Reiner, Pacific Southwest Region
(Resident Fish Program)
Lake Tahoe Basin Management Unit
870 Emerald Bay Rd., Suite 1
South Lake Tahoe, CA 96150

Region 6

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Wildlife, Fish & Botany Staff
Federal Office Building, Box 21628
Juneau, AK 99802-1628

Intermountain/Northern Region

Kerry Overton, Fish Research Work Unit
Intermountain Research Station
316 E. Myrtle St.
Boise, ID 83702

Associates

Glenn Chen
Fisheries Biologist/Monitoring Specialist,
USDA Forest Service
Fish & Wildlife Department
Utah State University
Logan, UT 84322-5210

Fred Mangum
Aquatic Ecosystem Analysis Lab
105 Page School
Brigham Young University
Provo, UT 84602

Ken Roby
Hydrologist, USDA Forest Service
Pacific Southwest Experiment Station
P.O. Box 245
Berkeley, CA 94701-0245

Larry Schmidt
Stream Systems Technology Center
USDA Forest Service
Rocky Mountain Experiment Station
240 W. Prospect
Fort Collins, CO 80526-2098

Mark Vinson
Hydrologist/Monitoring Specialist,
USDI Bureau of Land Management
Fish & Wildlife Department
Utah State University,
Logan, UT 84322-5210

Unfortunately, the methods used in movement studies favor relocating immobile fish (Gowan et al., in press). The procedure for most studies was to mark fish in relatively short reaches of streams, return to these same reaches weeks to a year later to resample them, then discuss only the recapture of marked fish. Usually few if any areas outside the selected reaches were sampled. Because most marked fish that were recaptured came from the reaches where they were originally marked, the authors considered this evidence for a lack of movement. But they typically failed to address the fate of the 15 to 90% of marked fish that were never recaptured, or attributed their absence to mortality or lost marks. Studies employing other techniques, such as direct observation, were handicapped because fish were not followed during all seasons or at night (e.g., Bachman 1984). Until the last five years, potential movement had been inadequately evaluated.

New Views of Movement

Recent research in the Midwest and the Rocky Mountains has disputed the paradigm of immobility of stream-dwelling trout. Clapp et al. (1990) and Meyers et al. (1992) used radiotelemetry to monitor the positions of large brown trout in Michigan and Wisconsin, and observed seasonal movements of over 30 km. Similarly, Young (in press) implanted transmitters in over 50 adult brown trout in tributaries of the North Platte River in Wyoming. I observed fish moving as far as 96 km and hypothesized that fish began spawning migrations from the river to the tributaries in late July, wintered in the tributaries (often in deep pools), and returned to the river during spring high flows (Figure 1). Young (in review) used the same technique to monitor much smaller Colorado River cutthroat trout (*O. c. pleutiticus*) and

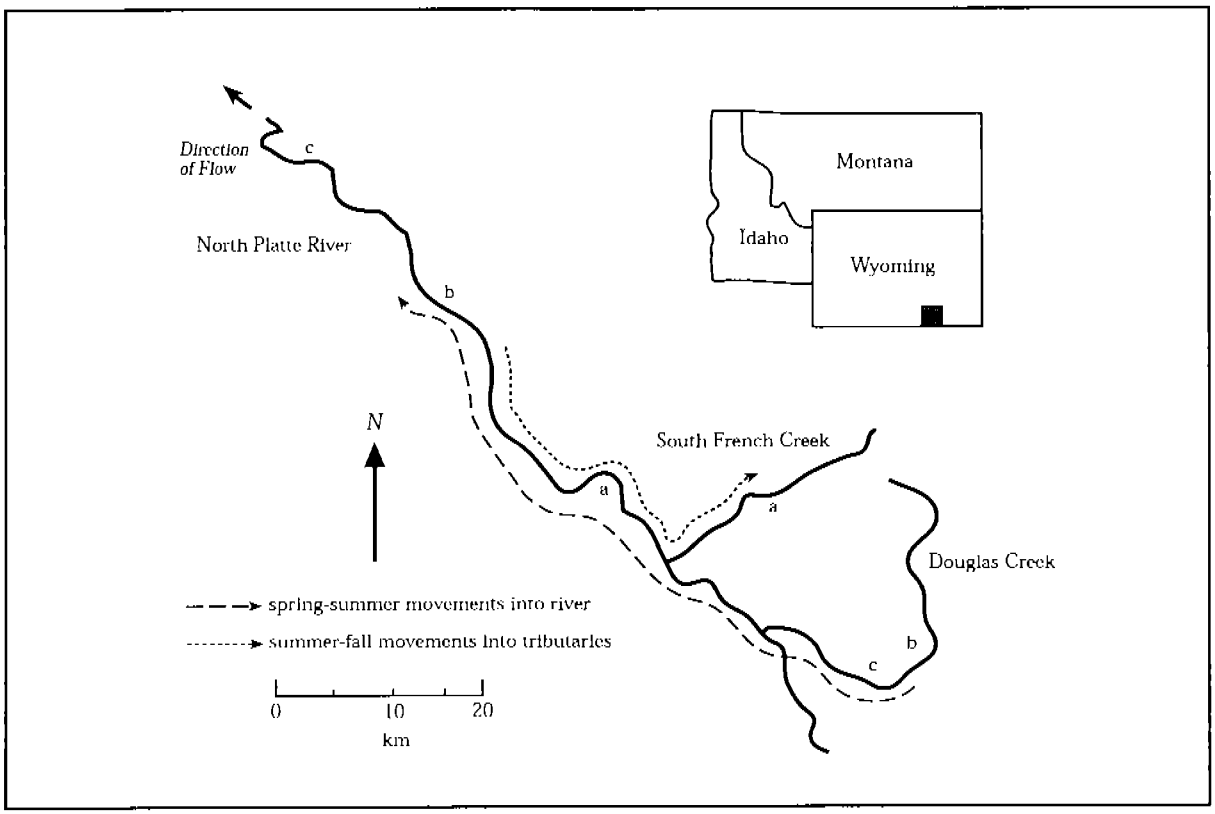

Figure 1. Brown trout movements in the North Platte River drainage. The dotted line represents hypothesized summer-fall movements into the tributaries, and the dashed line represents hypothesized spring-summer movements into the river. Small letters represent observed movements of three brown trout: fish "a" moved 23 km, fish "b" moved 66 km, and fish "c" moved 96 km.

detected movements averaging over 300 m (and up to 2.4 km) in mid-summer. Twenty-four-hour observations of both species revealed numerous movements of over 100 m and up to 1.1 km (Young, unpublished data). Using two-way fish traps to monitor movement, Riley et al. (1992) observed extensive, continuous movements of brook trout *(Salvelinus fontinalis)* in mid to late summer in small Colorado streams. Investigations of these species, as well as rainbow trout *(O. mykiss)* in Idaho (Middle Fork Salmon River, Bjornn and Mallet 1964; Silver Creek, Young, unpublished data), continue to demonstrate that movement is far more commonplace among adult trout than previously believed.

Consequences of Movement

Many aspects of resident trout biology implicitly rest on the assumption of immobility. If this assumption is invalid, it challenges several tenets of current trout management and research.

Special regulations.—Restrictive regulations are usually designed to reduce harvest of some or all of a trout population. These regulations presume that the protected groups will remain within designated stream reaches. But this presumption is not always correct; Clapp et al. (1990) noted that some large brown trout, originally tagged in a no-kill section of the South Branch of the Au Sable River, spent most of their time in a standard-regulation reach. In Wyoming, a slot limit has protected 254-406 mm trout in the North Platte River since 1982 (Mike Snigg, Wyoming Game and Fish Department, personal communication), and this may have led to increases in the abundance of spawning adults in the tributaries during the spawning run. The tributaries, however, are under standard regulations, and fluvial fish are unprotected once they enter the tributaries (often as early as July). If anglers harvest these large fish in the tributaries (and anecdotal evidence suggests that they do), future gains to the overall population may be limited.

Up- and downstream effects.—Another belief is the overriding importance of local habitat on fish populations. For example, structural rehabilitation has been thought to increase the abundance of trout in a treated reach by increasing survival, but this assumption has never been verified. In contrast, Riley and Fausch (in press) attributed the increased abundance of trout in structurally enhanced reaches of six Colorado streams to greater retention of mobile fish arriving from outside the treated reaches. This implies that the absence of a critical habitat outside an "enhanced" reach may be responsible for suboptimal trout densities within the reach. Consider that suitable edge habitat for fry of Colorado River cutthroat trout was usually unoccupied unless spawning habitat was nearby (Bozek 1990).

The possibility of fish movement is frequently ignored when building in-stream structures not intended to enhance trout populations (e.g., water diversions or dams). One consequence is that fish may be blocked from seasonally critical habitats up- or downstream (e.g., spawning or over-wintering sites). Alternatively, such barriers may cause the extinction of mobile life history forms, and if these forms are genetically distinct, their genetic contribution to the population will be lost. A genetic contribution to mobility is plausible but speculative (Jonsson 1985; Northcote 1992). Regardless, these structures fragment populations that then run a greater risk of extinction without the opportunity for natural recolonization.

Up- and downstream effects are not limited to physical disruptions. The stocking of non-native trout has led to the eventual loss of many indigenous trout populations, except where barriers prevented migration of the invading species (see Young 1995). For example, a single stocking of brook trout in a headwater lake apparently led to their eventual replacement of Colorado River cutthroat trout in most of the Battle Creek, Wyoming watershed, except where a polluted stream prevented their invasion into unpolluted tributaries (Eiserman 1958). Ironically, the relatively rapid spread of introduced populations was apparently disregarded as evidence that trout were mobile.

Sampling fish abundance and population characteristics.—Most estimates of fish abundance in streams are derived from one or a few short reaches of a stream, typically only once each year (or less often). Movement of fish through these reaches would render counts suspect, in part by violating an assumption of mark-recapture estimates. Decker and Erman (1992), after repeatedly electrofishing adjoining reaches of one stream throughout a summer, noted that the abundance of several trout species varied asynchronously. They attributed this variability to species-specific movements, and questioned the value of one-time sampling for estimating fish abundance. Over 50 years earlier, Shetter and Hazzard (1938) similarly concluded that "populations of stream fish are relatively unstable in specific areas of a stream during the summer months, and ... calculations of stream populations from counts made on one or two short sections of stream at only one period of the year are not reliable." Long-term modelling of population fluctuations (Platts and Nelson 1988) or community composition (Ross et al. 1985) are especially sensitive to annual or species-specific variation in mobility. Even one-time basin-wide inventories cannot account for trout mobility. Herger et al. (in review) performed two basin-wide surveys one month apart on each of two streams, and noted that the redistribution of Colorado River cutthroat trout led to different estimates of habitat-specific densities and overall trout abundance within each stream.

This unreliability can extend to other kinds of sampling. For example, meristic and morphometric analyses were used to determine the genetic purity of Colorado River cutthroat trout from two tributaries and the mainstem of the North Fork Little Snake River in southern Wyoming (Binns 1977). The analyses indicated that fish in the mainstem were genetically pure, fish from Harrison Creek were obviously contaminated by hybridization, and fish from Green Timber Creek were assumed to be intermediate. However, in movement studies conducted in 1992 (Young, in review), a single radio-tagged adult occupied all three locations within 23 days. Moreover, nearly all the fish originally captured in Harrison Creek and Green Timber Creek eventually migrated to the North Fork Little Snake River and could have been thought to represent the putatively isolated populations in any of the three streams. Because of the potential seasonal and annual variability in population composition, we should consider the consequences of one-time sampling for describing population genetic structure (Fausch and Young, in press).

Habitat modelling.—Modelling may also be confounded by trout movement. Many habitat-based models, constructed from physical or biological data often collected at a single point in time, attempt to predict the abundance or biomass of salmonids (see Fausch et al. 1988 for examples). The inability to incorporate temporal variation in stream characteristics has been recognized as a shortcoming of such models i.e., habitat characteristics change seasonally without apparent concurrent changes in fish abundance (Conder and Annear 1987). Yet rarely considered is the potential temporal variation in fish abundance produced by mobility, which could add substantially to the unexplained variation in such models. Additionally, that species (e.g., brown trout) may not be in feeding positions when sampled by electrofishing (Young, personal observation) may further degrade the performance of these models.

Arbitrary definition of populations.—Perhaps because of a perceived lack of mobility in fishes, biologists often attempt to geographically, but not biologically, define populations. That is, we often designate the trout in a small stream as a single population (in a sense, isolated by immobility). Yet rarely is this designation merited, because trout may immigrate to the small stream (to reproduce, feed, or escape floods) or emigrate from it (to overwinter or escape desiccation). That the range of a single population may include far more waters than the "type location" is consistent with the emerging concept of metapopulations. Metapopulations consist of a collection of subpopulations that are linked by immigration and emigration (Hanski and Gilpin 1991). The individual subpopulations may thrive, suffer losses of genetic variation, or go extinct, but individuals from other subpopulations within the

metapopulation can contribute to the growing subpopulations, restore genetic variation to small subpopulations, or found new subpopulations after extinction. To persist, metapopulations must consist of periodically mobile individuals in habitats without continuous barriers to movement (Gilpin 1987). Whether metapopulation theory explains trout population structure remains to be investigated, but it seems likely that most populations of salmonids have been founded by mobile individuals from large populations (cf. Milner and Bailey 1989).

Conclusions

A new paradigm for stream-dwelling trout considers (but does not mandate) mobility as one of the possible responses to food, growth, competition, predation, environmental disturbance, and daily and seasonal cycles. Movement may be minimal under some circumstances e.g., abundant macroinvertebrates, complex habitats, and environmental stability (cf. Bachman 1984). But because most streams are spatially and temporally heterogeneous, trout may elect to move frequently and extensively. The challenge for managers and researchers is to recognize when and where movement will be advantageous or necessary for maintaining wild trout populations.

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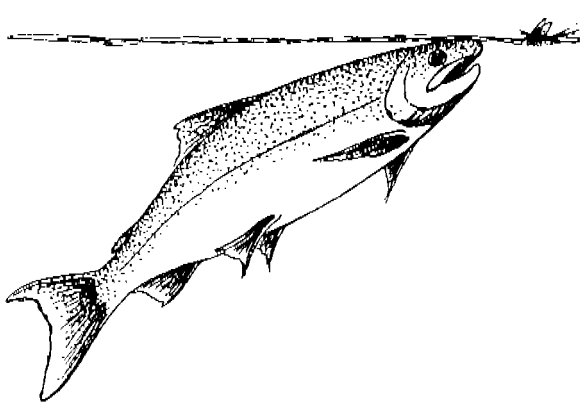

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