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Variable Migratory Patterns of Different Adult Rainbow Trout Life History Types in a Southwest Alaska Watershed

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Abstract.—Radiotelemetry was used to document population structure in adult rainbow trout *Oncorhynchus mykiss* from the Alagnak River, southwest Alaska. Rainbow trout (N = 134) longer than 440 mm were implanted with radio transmitters and tracked for varying periods from July 1997 to April 1999. Fifty-eight radio-tagged fish were tracked for sufficient duration (at least 11 months) to allow description of seasonal migratory patterns. Unique seasonal movements of fish suggested discrete, within-basin population structure. Telemetry data documented the existence of multiple migratory and nonmigratory groups of rainbow trout, indicating unique life history patterns. The observed groups consisted of what we defined as a lake-resident ecotype, a lake–river ecotype, and a riverine ecotype; the riverive ecotype demonstrated both highly migratory and nonmigratory movement behavior. Considerable variation in movement patterns was found within both the lake–river group and the river migratory group. Radio-tagged trout did not migrate between the two Alagnak watershed lakes in either year of the study, suggesting lake fidelity in the population structure. Alagnak River rainbow trout may have evolved the observed seasonal movement patterns to optimize winter thermal refugia and summer food availability of salmon eggs and carcasses.

The Alagnak River in southwest Alaska, designated a National Wild River by the U.S. Congress in 1980, supports natural, self-reproducing populations of rainbow trout *Oncorhynchus mykiss*. Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, coho salmon *O. kisutch*, pink salmon *O. gorbuscha*, and sockeye salmon *O. nerka*, as well as Arctic grayling *Thymallus arcticus*, Dolly Varden *Salvelinus malma*, and lake trout *S. namaycush* also inhabit the watershed and are targeted in the sport fishery (Dunaway 1990). Trophy rainbow trout fishing on the Alagnak River is world renowned, and the river is considered one of the most popular fly-in fishing destinations in southwest Alaska. Visitor use for all sportfishing has increased from approximately 1,900 angler-days per season in 1981 to 13,000 angler-days in 1995, and has remained stable thereafter (Jaenicke 1998a).

Concerns have been raised about the health of the rainbow trout population(s) in the Alagnak River and its tributaries upstream in Katmai National Park because of the dramatic increase in fishing pressure over the last decade. Angler complaints of poor fishing and a decrease in the average size of rainbow trout throughout the watershed are common (Jaenicke 1998b; J. Meka, personal observation). The estimated total number of angler-caught rainbow trout on the Alagnak River ranged between 6,057 and 30,665 fish per year in the 1990s, although the documented harvest rate has been less than 800 fish per year since 1981 (Jaenicke 1998a). The Alaska Department of Fish and Game invoked emergency regulations preventing the retention of any Alagnak River rainbow trout in 1996 and 1997 in response to increased fishing pressure. The Alaska Board of Fisheries established permanent regulations in 1998 that limited Alagnak rainbow trout sportfishing to catch and release only.

The effects of the increasingly popular Alagnak watershed rainbow trout sport fishery have been difficult to assess because knowledge of basic life history characteristics for this species in Alaska is limited. Fundamental questions about population structure in Alagnak River rainbow trout need to be addressed before assessments of population status can be initiated. For example, it is unknown whether rainbow trout in the various rivers, lakes, and tributaries of the watershed are a single, mixed

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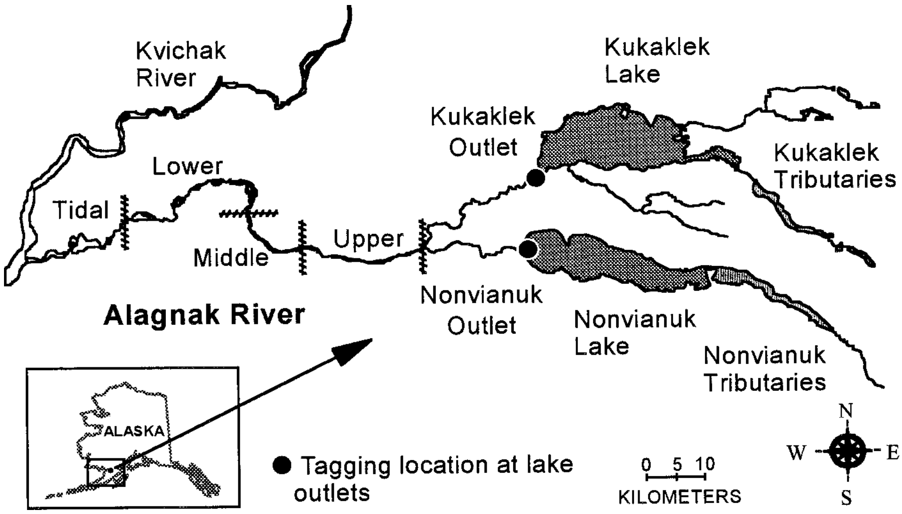

FIGURE 1.—Map of the Alagnak River drainage. Rainbow trout were captured and implanted with radio transmitters in 1997 and 1998 within the tidal, lower, middle, and upper habitat zones and at the Kukaklek and Nonvianuk Lake outlets. Solid circles indicate tagging locations at lake outlets.

population with interbreeding spawning groups, or whether there are discrete spawning populations representing different temporal or spatial groups.

It is generally agreed that seasonal migrations occur in Alagnak River rainbow trout, yet little is known about the detailed movement patterns and population intermixing within the basin. In this paper, we adopt the definition of migration as that given for freshwater fishes by Northcote (1978): ''movements resulting in an alternation between two or more separate habitats (i.e., a movement away from one habitat followed eventually by a return again) occurring with regular periodicity (usually seasonal or annual, but certainly within the lifespan of an individual) and involving a large fraction of the population.'' Northcote (1978) also suggests that movement is directed, not random, and that passive drift may occur as part of a migration. Northcote (1997) refers to potamodromous migrations as cyclic, evolving to optimize feeding opportunities, survival, and reproductive success.

The objectives of this study were to (1) use radiotelemetry to describe the extent and patterns of movement of rainbow trout in the Alagnak watershed, (2) determine whether movement patterns exhibited by Alagnak River rainbow trout suggest unique life histories for separate groups of fish, and (3) examine the differences in temporal and spatial movements among groups of radio-tagged rainbow trout. We also discuss how this information provides a framework for addressing rainbow trout fisheries management issues on the Alagnak River and potentially other watersheds in southwest Alaska.

Methods

Study site.—The Alagnak River originates at the outlet of Kukaklek Lake and flows 120 km into the Kvichak River, which drains into Bristol Bay (Figure 1). The major tributary is the Nonvianuk River, which originates at Nonvianuk Lake south of Kukaklek Lake. Numerous tributaries feed into Kukaklek and Nonvianuk lakes, the largest of which are the Kulik River, Battle Creek, and Moraine Creek. The Alagnak River is multibraided downstream of the confluence with the Nonvianuk River, with few significant tributaries, and eventually becomes tidally influenced near its union with the Kvichak River. All but the downstreammost 29 km of the Alagnak River are managed by Katmai National Park, headquartered in King Salmon, Alaska. The majority of the upper watershed is within the Katmai National Preserve or Katmai National Park.

We categorized the watershed into 12 habitat zones, or sections, based on general stream geomorphology to facilitate analysis of the results. We believed a priori that the zones might influence the distribution of rainbow trout. Delineation of the zones began at the mouth of the Alagnak River and moved upstream: tidal, lower, middle, and upper main stem, Nonvianuk River, Nonvianuk outlet, Nonvianuk Lake, Nonvianuk Lake tributaries, the Alagnak River above the confluence with the Nonvianuk River, Kukaklek outlet, Kukaklek Lake, and Kukaklek Lake tributaries. Rainbow trout were captured in six of the most accessible habitat zones where the trout fishery is most concentrated (Jaenicke 1998a, 1998b; Meka, personal observation). Tagging zones were the Kukaklek Lake and Nonvianuk Lake outlets, and the upper, middle, lower, and tidal zones within the main stem below the confluence with the Nonvianuk River. Within the main stem, the tidal section is generally one meandering channel that is tidally influenced; the lower zone is made up of several large, meandering channels; the middle zone is heavily braided with several main channels, multiple small channels, and numerous islands; and the upper zone has numerous islands with one or two main channels. In this paper, we will refer to the upper portion of the lower zone, the middle zone, and the lower portion of the upper zone as the braided reaches. The Kukaklek and Nonvianuk lakes are in upland tundra, and their outlet rivers (above the confluence) each have one main channel with numerous islands.

Sampling procedures and implantation of transmitters.—Our study focused on large rainbow trout (>440 mm) because they are targeted in the Alagnak River trout sport fishery and because we believed they would be the least affected by tagging. Adult rainbow trout were caught by hook and line and by seining, and fish over 440 mm were implanted with radio transmitters in July and October 1997 and from April 15 to May 7, 1998. In 1997, fish were captured after the spawning period (May to early June), whereas in 1998 prespawning aggregations were targeted so that dispersal of possible spawning subpopulations could be monitored.

Individual transmitters were tested for functionality before each surgery. Rainbow trout were anesthetized with a 100-mg/L solution of tricaine methanesulfonate (MS-222). Fish were placed ventral side up in a neoprene-lined cradle during surgery, with the head slightly higher than the tail to prevent antiseptic from entering the gills and to allow the gill bath to moisten the sides of the fish. The fish received a steady gill bath of either oxygenated water, or the MS-222 solution if movement occurred during the procedure. A 2–3-cm incision large enough to accommodate the transmitter was made anterior to the pelvic girdle, 1–2 cm from the midventral axis. An additional incision (about 1 cm) was made anterior to the vent to allow insertion of the grooved director, a slender metal device approximately 10 cm in length. A hypodermic needle was routed through the first incision until the tip of the needle made contact with the grooved director, and the needle was guided until its tip exited the second incision. The antennae was inserted through the needle until it emerged from the second incision, at which time the grooved director and needle were removed and the radio transmitter was inserted lengthwise through the original incision. A dose of oxytetracycline (0.5 mg/kg body weight) was injected into the first incision to help prevent infection. The first incision was closed with three to five stitches of absorbable clear or black monofilament suture and sealed with two to three drops of Vetbond adhesive. Fish were returned to a freshwater holding tank until they swam upright and were placed in a mesh-surrounded holding tank within the river until equilibrium was reached. Each surgery averaged 5–6 min, and fish were ready for release 20–30 min from the start of surgery. In both years, the application of transmitters was similar to standard surgical implant methods used by Summerfelt and Smith (1990).

The transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota) used in 1997 and 1998 were 56 mm long, contained a 3.5-V battery, and were encapsulated in an electric resin epoxy. Each tag weighed 10.4–11.4 g in air and never exceeded 2% of fish weight (Winter 1983). A 26-cm flexible external whip antenna was attached to one end of each tag. Standard beeper tags (model 1035) with unique frequencies ranging between 40 and 41 MHz were used in 1997. Pulse-coded tags (model 1035) were used in 1998, with 10 individually encoded tags within each of 10 unique frequencies ranging between 40 and 41 MHz (100-tag potential). A 2-MHz receiver (model R2100) was used for relocating transmitters in 1997, and tags released in 1998 were identified with a data logger (DC II model D5041) and receiver set.

Radio-tracking procedures.—Radio-tagged rainbow trout were relocated with a combination of aerial and boat tracking surveys. Aerial telemetry surveys of the Alagnak River main stem, the Kukaklek and Nonvianuk lakes, and the inlet tributaries of the watershed were conducted once per month, weather permitting, from July 1997 to April 1999. The aerial surveys were conducted from fixed-wing aircraft equipped with tuned-loop antennae attached to each wing strut. Flights along the main-stem river averaged 300 m above ground in 1997 and 180 m above ground in 1998 and 1999; flights over the lakes averaged 300 m above ground in all years. Boat surveys were conducted from July to October 1997 and from May to September 1998. The main stem from the confluence with the Nonvianuk River to the mouth of the Alagnak River was boat surveyed, on average, every 2–3 d. Final determinations of tag location depended on the observer deciding where the peak signal occurred. Therefore, boat relocations were considered more accurate than aerial relocations due to increased proximity to radio-tagged fish. The majority of locations of radio-tagged fish were recorded with a portable global positioning system (GPS) unit; written descriptions of the area were substituted when the GPS unit was unavailable or not functioning. All relocations were converted to latitude and longitude, with the accuracy depending on the method of relocation.

If there was no detected movement from a radio-tagged rainbow trout after three consecutive boat relocations, we attempted to gain a visual observation of the fish or to recover the radio tag. In areas only accessible by plane, a radio-tagged fish that remained ''inactive'' and made no detected upstream movement after three consecutive aerial surveys was considered dead or to have expelled its tag at the location of its last previous upstream movement. Tracking of a radio tag ceased *only* after the transmitter was recovered during a ground survey. Tags that were not relocated for six consecutive months were considered to have failed and were recorded as ''missing.''

Geographical analysis of fish movement was done with ArcInfo software (ESRI, Redlands, California). A geographical information systems (GIS)-based vector map of the Alagnak watershed was digitized, and reference points were made every 100 m along the streams and lakes, starting with zero at the mouth of the Alagnak River and increasing upstream into the inlet tributaries of both Kukaklek and Nonvianuk lakes. Two pathways in each lake were digitized with reference points every 100 m from the outlet of each lake to the inlet tributaries. Horizontal movements of fish within the lakes were not accounted for. Each fish relocation was associated with the nearest reference point to determine the fish's position in the watershed. This mapping system was used as a base reference to determine the distance and direction of movements.

Definition of criteria for data analysis.—To analyze the telemetry data from only those rainbow trout with the most consistent relocation data over time, we divided each year into three seasons based upon estimated seasonal histories for salmonids and rainbow trout in southwest Alaska (Northcote 1978; Burger and Gwartney 1986; Adams 1996, 1999; Palmer 1998). These periods also include the months in which migrations to spawning and winter habitats may occur (April and October): (1) spawning (April 1 to June 30), (2) postspawning−feeding (July 1 to September 30), and (3) winter (October 1 to March 31).

Fish with at least one relocation per month for two separate months during the spawning period (1998) and with observations in at least one postspawning period (1997 or 1998) and at least one winter period (1997–1998 or 1998–1999) were included in the analysis. Many fish did not meet these criteria and were dropped from further analysis, resulting in a conservative data set that included only those fish with sufficient data to allow us to draw conclusions about movement patterns.

Seasonal movement.—Migratory groups of rainbow trout have been described in the literature for the reproductive migrations in Yellowstone Lake cutthroat trout *O. clarki* (Varley and Gresswell 1988) and for reproductive, trophic, and refuge migrations in other potamodromous salmonids (Northcote 1997). We began by analyzing the movement of radio-tagged rainbow trout throughout their tracking histories to determine whether they were relocated solely within the habitat zones where they were captured. If movement to other zones was detected, similar patterns of movement for fish captured in the same zones were examined to determine whether tagging location was indicative of specific movement patterns.

Individual movement plots were created to graphically depict where in the watershed (i.e., river kilometer [rkm], from the mouth of the river) each fish was located over time. By visually examining each movement plot, we were able to spatiotemporally distinguish three different groups of fish (e.g., Figure 2). The groups included: (1) fish that were relocated entirely within the main-stem Alagnak River, (2) fish that remained in either Kukaklek Lake or Nonvianuk Lake and occasionally their tributaries, and (3) fish that were relocated both within a lake and the main-stem Alagnak River, and occasionally the lake tributaries. We further defined our migratory groups, or ecotypes, of radio-tagged rainbow trout based on descriptions from the literature.

(1) Lake-resident fish, referred to as lacustrine or lacustrine–adfluvial by Varley and Gresswell (1988), used one of the two lakes and their respective outlets, with some use of the inlet tributaries. None of the lake-resident fish were ever

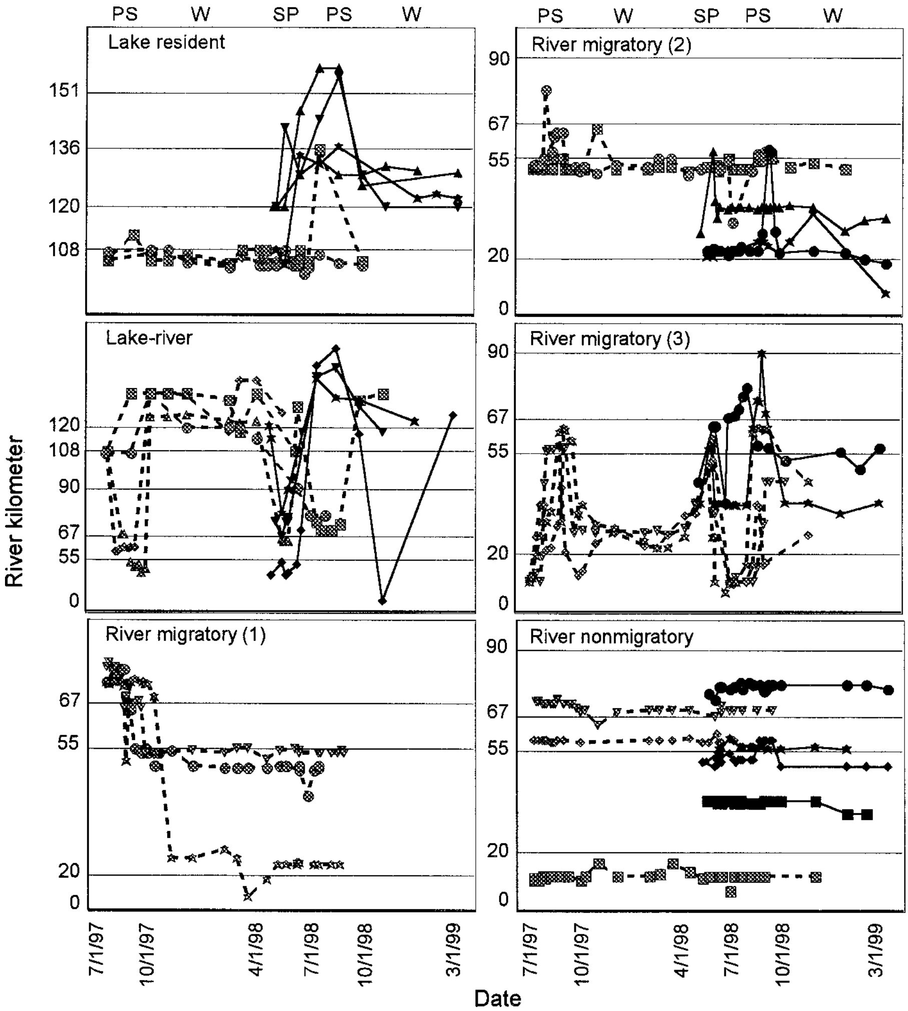

FIGURE 2.—Individual fish relocations throughout the Alagnak River drainage. The *y*-axis scale for each graph represents the river kilometer (rkm, from the confluence with the Kvichak River) in which each individual radio-tagged fish was relocated (Figure 1) (rkm 0–20 = tidal habitat zone, rkm 21–55 = lower habitat zone, rkm 56–67 = middle habitat zone, rkm 68–90 = upper habitat zone, rkm 108 = Nonvianuk Lake outlet, rkm 120 = Kukaklek Lake outlet, rkm 136 = Nonvianuk Lake tributaries, and rkm 151 = Kukaklek Lake tributaries). The *x*-axis represents the relocation dates. Note that the *y*-axis scale varies with ecotype. Each line represents an individual fish, and the markers within each line indicate relocations over time. The dotted lines with gray markers represent rainbow trout tagged in 1997, and the solid lines with black markers indicate rainbow trout tagged in 1998. Each graph is divided into seasons, with the season labels at the top of the figure (PS = postspawning, W = winter, and SP = spawning). Because of the large number of fish from the river migratory (patterns 1, 2, and 3) and nonmigratory groups, only a few representative fish from each group are included in the graphs to facilitate display; the chosen individuals demonstrated behavior typical of their respective groups.

relocated more than 5 km below the lake outlets. Feeding and refuge habitats were generally situated in the lakes, and spawning habitat was generally situated in the inlet tributaries (Northcote 1997).

(2) Lake–river fish, referred to as allacustrine by Varley and Gresswell (1988), migrated between the lakes and their outlet rivers, and some also used the inlet tributaries. Their feeding and refuge habitats were generally situated in the lakes, and spawning habitat was in the outlet rivers (Northcote 1997).

(3) Riverine fish, referred to as fluvial by Varley and Gresswell (1988), remained entirely within the

TABLE 1.—Number of radio-tagged rainbow trout (n = 135) in each habitat section of the Alagnak River watershed in 1997 and 1998. The number of fish that met the criteria for analysis (see Methods) is given in parentheses.

Month tagged	Main stem				Lake		Total
	Tidal	Lower	Middle	Upper	Kukaklek	Nonvianuk	
Jul 1997	10 (6)	9 (7)	3 (3)	8 (7)	10 (0)	10 (7)	50 (30)
Oct 1997		5 (2)		4 (0)			9 (2)
Apr–May 1998		28 (18)	4 (1)	3 (2)	21 (4)	20 (1)	76 (26)
Total	10 (6)	42 (27)	7 (4)	15 (9)	31 (4)	30 (8)	135 (58)

main stem and demonstrated a continuum of movement behavior. Thus, we subdivided riverine fish into migratory and nonmigratory groups. Migratory fish were those with a total range greater than 10 km, and nonmigratory fish were those with a total range less than 10 km (Wenger et al. 1985; Brown 1994; Swanberg 1997; Schmetterling 2001).

To reaffirm successful identification of groups with different migratory attributes, we calculated the following descriptive variables and compared them among the three ecotypes. The mean relocations (mean river kilometer of sites where fish were located) of rainbow trout within each ecotype during all seasons were examined to determine differences in seasonal distribution. This was necessary because the number of relocations per individual fish varied greatly within each month, particularly during the summers, when tracking was conducted almost daily on the main stem and monthly in the lakes. Mean total range, defined as the difference between the farthest upstream and downstream relocations for each fish within a season, was calculated for all fish within each ecotype. Estimated average maximum distances fish moved from one season to the next (e.g., movement from spawning 1998 to postspawning 1998) were compared among groups. These descriptive variables were not tested statistically because they were based on the subjective categorization of ecotypes determined from our observations of the data.

To test for interbasin mixing, we compared the distributions of the lake–river and lake-resident fish to determine whether the fish moved between the Kukaklek and Nonvianuk drainages. The movement of fish captured in 1997 that were relocated in two postspawning or winter seasons was examined to reveal any patterns of repeated site fidelity to summer and winter habitat. We did not observe individual rainbow trout spawning in this study, but we assumed that one-way migrations greater than 10 km within the spawning period with a subsequent return were made by fish moving to suitable spawning habitat, based on general descriptions of trout spawning migrations in the literature (Northcote 1991).

In addition to our migratory ecotype classification based on visual examination of movement plots, we subjected the data to a cluster analysis. Because tracking dates and the number of relocations varied among fish included in the analysis, the total range in each season was used to reflect the extent of seasonal movement of fish throughout the watershed. The data used in the cluster analysis included the minimum and maximum river kilometer location during the spawning, postspawning, and winter seasons. For fish captured in 1997 with relocation data in two postspawning or winter seasons, the smallest minimum and largest maximum seasonal relocations of the two years were used in the cluster analysis. Results from the cluster analysis were then compared to the literature-based, observational grouping criteria.

Results

Radiotelemetry

A total of 135 fish were tagged during the study. Fifty-nine radio transmitters were implanted into rainbow trout in six sections of the watershed in July and October 1997; 32 (54%) of the 59 radio-tagged fish provided relocations of sufficient duration for long-term analysis (Table 1). Twenty-five (42%) of the 59 fish were considered to have died or to have expelled their tags by the summer of 1998. The tags were recovered along the riverbanks, on gravel bars, or buried in the riverbed; no carcasses were ever found with or near the tags. Three fish (5%) were assumed to have experienced tag failure because contact was lost immediately after surgery. Fourteen fish (24%) were assumed to have experienced tag failure or to have left the system after the spring or summer of 1998, and were never relocated again. Seventy-six rainbow trout were implanted with transmitters within the same six sections of the watershed from April 15 to May 13, 1998. Twenty-one (28%) of the 76 fish either died or expelled their tags during the summer of 1998,

TABLE 2.—Number of radio-tagged rainbow trout (n = 58) in each ecotype captured within each Alagnak River habitat zone in 1997 and 1998. Only those fish that met criteria for analysis are included.

Ecotype	Main stem				Lake	
	Tidal	Lower	Middle	Upper	Kukaklek	Nonvianuk
Lake resident (n = 7)					3	4
Lake–river (n = 7)		1		1	1	4
River migratory (n = 34)	5	21	2	6		
River nonmigratory (n = 10)	1	5	2	2		

and another 19 fish (25%) experienced tag failure within the first 6 months after release. In all, 26 (34%) radio-tagged fish in 1998 provided sufficient relocations for long-term analysis.

The number of relocations per fish varied because the main stem was surveyed by boat two to three times per week during the summers of 1997 and 1998, and the entire watershed was surveyed by plane usually once per month from July 1997 to April 1999. Tracking of radio-tagged fish captured in 1997 ceased in February 1999 due to expected battery expirations. All radio-tracking ceased in April 1999 because so few functional transmitters remained.

Definition of Migratory Ecotypes of Radio-Tagged Rainbow Trout

Fifty-eight radio-tagged rainbow trout met our criteria of having at least one relocation per month for two separate months during the spawning season and at least one postspawning relocation and one winter season relocation. Preliminary investigation of results indicated that movement patterns were not necessarily related to tagging location, and movement patterns for individual fish were not predicted by tagging location. When each fish was grouped into one of the three ecotypes depending on recorded migratory behavior, it became apparent that radio-tagged fish within the same ecotype were not necessarily captured in the same location (Table 2). Movement was greater in the spawning and postspawning periods for the majority of fish, regardless of where they were captured or relocated in the watershed. It was obvious that there was great variation in movement patterns among many radio-tagged fish throughout the drainage. Our data allowed descriptive separation of the three ecotypes based on visual examination of individual movement plots, comparison of calculated group attributes, and the cluster analysis.

Lake-resident ecotype.—Lake-resident rainbow trout (n = 7) were captured at the outlets of Kukaklek or Nonvianuk lakes and were found to use a combination of one of the lakes and the respective lake outlet and inlet tributaries (Figure 2). Two of the three fish captured at Nonvianuk Lake outlet in July 1997 remained near the outlet throughout their tracking histories. The remaining five fish used one of the two lakes (Nonvianuk [n = 2], Kukaklek [n = 3]) and showed greater movement during the 1998 spawning and postspawning seasons while making upstream migrations (range, 27–39 km) from the lake outlets into the lakes. Four of the five fish used the inlet tributaries. Each fish returned downstream (14–36 km) to overwinter near the outlet or in the lake.

Lake–river ecotype.—Rainbow trout within the lake–river ecotype (n = 7) used the lakes, inlet tributaries, and the Alagnak River main stem (Figure 2). Fish within this group were caught at the lake outlets and in the main stem in 1997 and 1998 (Table 2). Four lake–river trout used Nonvianuk Lake, three used Kukaklek Lake, and all used the main stem during some part of the year. Although rainbow trout from both lake systems used the braided reaches of the main stem during the spawning and postspawning periods, fish returned to their respective lake basins. There were no recorded movements between the two drainages.

Four fish captured at Nonvianuk Lake outlet in July 1997 used Nonvianuk Lake. Two of the four fish migrated downstream (47–69 km) from the outlet to the braided reaches of the main stem during the 1997 postspawning season, and returned to overwinter in Nonvianuk Lake. The other two fish moved upstream into the lake after tagging and remained there for the postspawning and winter periods. During the 1998 spawning period, one fish remained in the lake, one fish was located at the lake outlet, and two fish moved downstream (42–60 km) to the braided reaches of the main stem. By the 1998 postspawning season, contact had been lost with two fish and the remaining two were both relocated in the braided reaches. There was only one remaining fish with a functional transmitter during the 1998–1999 winter season, and that fish returned upstream (63 km) to overwinter in Nonvianuk Lake and its inlet tributaries. The two lake–river rainbow trout that used Nonvianuk Lake in both the 1997 and 1998 postspawning seasons did not exhibit site fidelity to suspected feeding areas.

The three rainbow trout that used Kukaklek Lake were captured during the 1998 prespawning season in the upper and lower sections of the main stem and at the Kukaklek Lake outlet. During the spawning season, the fish caught at the outlet moved downstream (43 km) into the braided reaches of the main stem. All three fish moved upstream (66–102 km) during the 1998 postspawning season from the braided reaches into Kukaklek Lake, and two of these fish continued to move upstream into the inlet tributaries. All three fish overwintered in Kukaklek Lake, yet one also made a downstream movement of 81 km from the lake to the lower section of the river in October 1998 and was relocated again in the lake 4 months later. The two fish that were tagged in the main stem were likely caught during their downstream migration from Kukaklek Lake to main-stem spawning grounds, perhaps just prior to spawning.

River ecotype.—The river ecotype (n = 44) represented the largest group of radio-tagged rainbow trout from this study, presumably because the majority of fishing effort in 1997 and 1998 was concentrated in the main stem from the tidal section up to the confluence with the Nonvianuk River. Fish within the river ecotype demonstrated both highly variable seasonal migratory behavior (n = 34), as well as nonmigratory behavior (n = 10). All nonmigratory fish, however, were observed to make upstream or downstream movements similar to the other ecotypes, but on a relatively smaller scale.

Rainbow trout considered migratory remained entirely within the main stem throughout their tracking histories, and each had a total range of greater than 10 km. River migratory fish were captured in four different main-stem habitats but did not necessarily exhibit fidelity to the tagging location. We found that fish movement was most variable within this group, and that many fish exhibited migrations within the lower, middle, and upper sections of the main-stem river during the spawning and postspawning seasons. River migratory fish exhibited three main migratory patterns.

Pattern 1 was observed in eight fish caught in the upper, middle, and lower sections of the river during the 1997 postspawning season (Figure 2). Fish left their tagging locations and migrated downstream (12–49 km) to the areas where they remained during the winter. During the spawning season, all fish remained close to their overwintering grounds, the majority of which were in the braided reaches.

Pattern 2 was observed in 13 fish caught in the lower and middle sections of the river in both tagging years. These fish were observed to make upstream and downstream migrations, yet they remained relatively close to their respective tagging sites for the majority of their tracking histories (Figure 2). Migrations occurred during all seasons. In general, fish within this group migrated upstream or downstream from their tagging areas and returned to these areas following the migration, indicating some degree of site fidelity to their respective tagging locations. Nine fish made upstream (5–28 km) or downstream (10–28 km) movements from their tagging areas during the spawning or postspawning periods, generally with return movements to the same areas. Four fish made upstream (19–26 km) or downstream (13–14 km) movements during one of the winter seasons, also with subsequent return movements. Two fish that were tracked for two postspawning seasons (one of which was tracked for two winter seasons) showed site fidelity to their tagging locations.

Pattern 3, the most diverse river migratory pattern, was observed in 13 fish caught in the lower and tidal sections of the river during 1997 and 1998 (Figure 2). Several fish caught in 1997 used the same areas during the 1997 and 1998 postspawning and winter periods, indicating some degree of fidelity to feeding and refuge habitats. Four of the 13 fish were caught on the same date in July 1997 at the same location in the tidal section. All four fish moved upstream (21–51 km) from their tagging sites to the braided reaches of the river during the 1997 postspawning season, with a subsequent downstream return (16–30 km) to the lower river, where they remained for the winter season. During the spawning period, all four fish moved upstream (10–33 km) from the areas in which they wintered to the braided reaches, and all returned downstream (21–50 km) to the tidal section near their tagging locations. In the 1998 postspawning period, all four fish moved upstream (21–57 km) once again, with two remaining there for winter 1998–1999 and two returning downstream (12–18 km) to overwinter. All four fish overwintered in the lower river during 1997–1998 and 1998–1999, and two of the four fish overwintered in the same areas during both years. Three of the four fish used

TABLE 3.—The mean river kilometer (± SD) where radio-tagged rainbow trout were relocated throughout their tracking histories, the mean total range (difference between the upstream-most and downstream-most relocations) for fish within each ecotype during each season, and the average maximum distance (km) fish moved from one season to the next for each ecotype (PS97 = postspawning 1997; W97–98 = winter 1997–1998; SP98 = spawning 1998; PS98 = postspawning 1998; and W98–99 = winter 1998–1999).

	Lake		River	
Comparison	Lake resident	Lake–river	Migratory	Nonmigratory
Mean relocation in watershed				
PS97	107.3 (0.8)	96.7 (29.7)	53.0 (15.1)	49.7 (22.5)
W97–98	106.0 (0.3)	126.7 (6.2)	42.3 (15.4)	49.8 (21.0)
SP98	116.0 (11)	95.7 (28.4)	41.5 (15.2)	52.1 (17.6)
PS98	133.5 (19.6)	117.5 (40)	44.6 (12.7)	52.2 (21.6)
W98–99	118.9 (11.4)	119.8 (18.6)	40.1 (9.6)	50.9 (16.8)
All seasons	118.6 (15.2)	109.6 (28.7)	43.8 (13.9)	50.6 (19.0)
Mean total range				
PS97	3.1 (3.6)	52.7 (27.3)	25.4 (15.8)	2.8 (2.4)
W97–98	3.7 (0.7)	12.0 (12.1)	10.0 (8.2)	3.1 (2.7)
SP98	14.1 (12)	28.8 (16.6)	13.7 (13.1)	3.8 (2.4)
PS98	9.2 (11.4)	5.3 (3.6)	16.8 (18.4)	2.3 (3.0)
W98–99	2.6 (3.3)	29.0 (40.8)	7.5 (6.9)	1.3 (1.6)
All seasons	7.6 (9.5)	25.1 (25.7)	14.4 (14.4)	2.7 (2.4)
Average maximum distance moved from one season to the next				
PS97 to W97–98	5.1 (2.1)	51.2 (33.0)	28.6 (13.1)	4.7 (3.4)
W97–98 to SP98	4.0 (2.3)	35.9 (16.6)	16.5 (11.5)	5.5 (2.9)
SP98 to PS98	26.3 (13.7)	72.4 (26.4)	23.6 (16.8)	4.4 (2.8)
PS98 to W98–99	20.3 (15.1)	60.2 (45.7)	23.5 (15.2)	3.3 (3.0)

the same postspawning areas during the 1997 and 1998 seasons.

The remaining nine fish from river migratory pattern 3, and from both tagging years, exhibited migratory behaviors similar to those of the other four fish, yet they were not captured at the same locations as the other fish. All made upstream migrations (5–57 km) followed by downstream return movements (4–52 km) during the spawning or postspawning periods or both, and all overwintered in the lower river.

Rainbow trout exhibiting river nonmigratory behavior (n = 10) remained entirely within the Alagnak River main stem and moved within a range of less than 10 km throughout their tracking histories (Figure 2). These fish exhibited fidelity to their tagging areas, with increased movement during the spawning and postspawning seasons. Eight fish remained in the braided reaches throughout their tracking histories, one fish remained in the lower section where the river becomes a meandering channel, and one fish remained in the tidal section. The majority of nonmigratory fish resided in the areas of the river to which the river migratory fish made upstream migrations during the spawning and postspawning seasons, and to which the lake–river fish made downstream migrations during the same seasons.

Comparisons among Ecotypes

Observations of migratory attributes across ecotypes (mean relocation, mean total ranges per season, and the maximum distance fish moved between consecutive seasons) were used for intergroup comparisons (Table 3).

Mean relocation.—There were substantial differences in the mean relocations among ecotypes in all seasons (Table 3). The lake–river and lake-resident groups were located farther upstream than the riverine groups (migratory and nonmigratory analyzed separately). There was also a general seasonal trend for the mean relocation within the lake-resident, river migratory, and river nonmigratory ecotypes to be farther upstream during the spawning and postspawning seasons than in other seasons. This was due to a general upstream movement during these seasons, followed by a general downstream relocation during the winter, presumably due to migration downstream from spawning and feeding areas to overwintering habitat. The mean relocations of lake–river fish indicated downstream movement during the spawning and postspawning seasons and upstream movement in the winter, when fish migrated into the lakes. Differences in the mean seasonal relocations among groups closely reflected the different migratory patterns we observed within each ecotype.

Total range and maximum movement between seasons.—The mean total range for the lake–resident fish during the 1997 postspawning season, winter 1997–1998, and winter 1998–1999 was small because fish stayed relatively close to the lake outlets and exhibited little movement (Table 3; Figure 2). The total range increased during the 1998 spawning and postspawning seasons, when fish migrated upstream to the inlet tributaries. The maximum distance moved between seasons was greatest from the 1998 spawning to postspawning seasons, when fish moved upstream into the inlet tributaries, and from the 1998 postspawning season to winter 1998–1999, when fish moved downstream from the inlet tributaries to the lake.

The lake–river fish had the largest total range during the 1997 postspawning and 1998 spawning seasons because fish made downstream migrations within those seasons into the Alagnak River main stem (Table 3; Figure 2). Although the distribution of fish ranged from the upper river to the inlet tributaries during the 1998 postspawning period, the range was low because radio-tagged fish made little or no documented movement within that season. Most lake–river fish exhibited little movement during winter 1997–1998, yet the winter 1998–1999 total range was large because one fish moved downstream 81 km from the Nonvianuk Lake outlet to the lower river, and back upstream to the lake during that season. The maximum distance moved between seasons was greatest from the postspawning to winter seasons, when fish made upstream migrations from the main-stem Alagnak River to the lakes, and from the winter to the spawning or postspawning seasons (1998), when fish migrated downstream from the lakes to the main stem.

The total range of river migratory fish was greatest during the postspawning and spawning seasons, when upstream migrations to the braided reaches were common, whereas the movement of these fish during the winter seasons was more restricted (Table 3; Figure 2). The maximum distance moved between seasons for the river migratory fish was greatest from the postspawning to winter seasons and from the spawning to postspawning seasons because fish made upstream migrations during the former seasons and returned downstream during the latter seasons. River nonmigratory fish maintained a small total range during all seasons, with a slight increase in range during the spawning season (Table 3; Figure 2). The maximum distance moved between seasons for nonmigratory fish was greatest from winter 1997–1998 to the 1998 spawning season.

Comparisons among ecotypes indicated that the average total range of movement was greatest for lake–river fish in all seasons except the 1998 postspawning season (Table 3), and the lake–river fish also moved the most from one season to the next. The river migratory fish generally exhibited the second greatest average range of movements in all seasons and the second greatest movement from one season to the next. The river nonmigratory fish exhibited the smallest range of movement in all seasons. River nonmigratory fish had the least movement from one season to the next, except from winter 1997–1998 to the 1998 spawning season, when lake-resident fish apparently moved less.

Cluster Analysis

Results from the cluster analysis reflected the spatial differences and general migratory patterns among ecotypes. Because relocation data varied each month due to tag failures, mortalities, and variable tracking effort, the minimum and maximum river locations (rkm) during one spawning, one postspawning, and one winter season were assumed to be the most reliable for use in the cluster analysis. The first cluster level separated the river fish from the lake-resident and lake–river fish (Figure 3). Within the lake-resident and lake–river fish cluster, the two main subgroups were (1) fish that used the Kukaklek Lake outlet, inlet tributaries, and main-stem Alagnak River, and (2) fish that used the Nonvianuk Lake outlet, inlet tributaries, and main-stem Alagnak River. Within the two lake subgroups, the analysis further clustered fish into those that used the lake and inlet tributaries, and those that used the lake, lake outlet, and main stem. One fish, which was captured at Nonvianuk Outlet and which made an 81-km migration downstream from the lake to the lower river and back again during winter 1998, formed its own cluster within the general lake group. The clustering process apparently first grouped the Kukaklek and Nonvianuk lakes' fish based on their geographic range and then created subgroups within each of the lake basin clusters based on the migratory characteristics of the lake-resident and lake–river ecotypes.

Within the river fish cluster, the two main subgroups were clustered by river location. The groups included (1) river migratory and nonmigratory fish that spent the majority of their time in the upper river section, the braided section, and the upper portion of the lower river, and (2) river

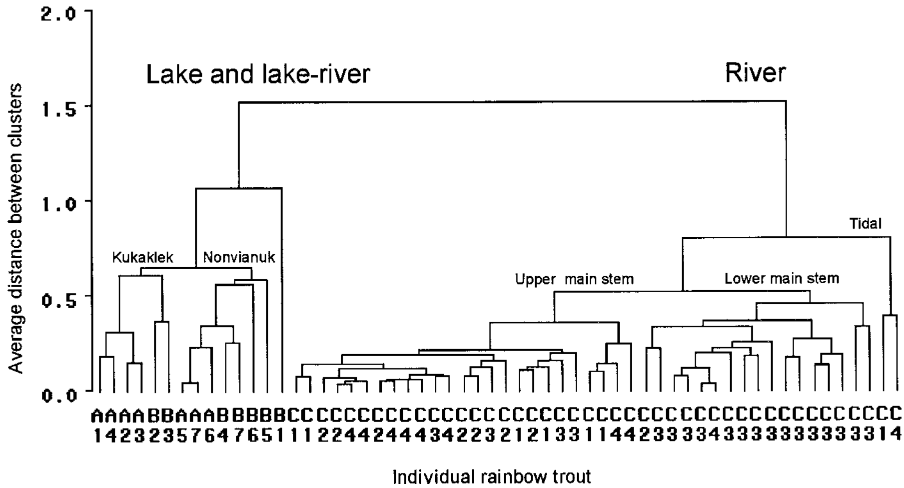

FIGURE 3.—Cluster analysis tree diagram of radio-tagged Alagnak River rainbow trout. The assigned ecotype for individual fish (*x*-axis) is included to compare grouping strategies between the cluster analysis and individual-movement graph approaches (A = lake-resident ecotype, B = lake–river ecotype, C1 = pattern-1 river migratory fish, C2 = pattern-2 river migratory fish, C3 = pattern-3 river migratory fish, and C4 = river nonmigratory fish). The numbers below groups A and B identify individual fish.

migratory and nonmigratory fish that spent the majority of their time in the lower river. Two outliers also formed an additional subcluster of fish that spent the majority of their time in the lowest, tidally influenced river reach. In general, river migratory pattern-1 and pattern-2 fish, plus the majority of nonmigratory fish, were included within the first river subgroup; the majority of river migratory pattern-3 fish were included in the second river subgroup. Therefore, the cluster analysis for riverine rainbow trout primarily reflected the general geographic range of fish, since pattern-1 and pattern-2 migratory fish and nonmigratory fish were located farther upstream in the watershed than pattern-3 migratory fish. Numerous subgroups were clustered within each of the two primary riverine groups, yet the small subgroups did not reflect the specific upstream and downstream migrations during the spawning and postspawning periods that we considered important for describing and identifying migratory and nonmigratory ecotype behavior. By examining the combined results of the fish movement graphs and cluster analysis, we were able to confidently identify rainbow trout ecotypes and describe the migratory and nonmigratory behavior of rainbow trout within each ecotype.

Discussion

The results from this study revealed unique, life-history-based, seasonal movements that suggest discrete, within-basin population structure of Alagnak River rainbow trout. Observed groups consisted of lake residents (lacustrine and lacustrine–adfluvial), a lake–river group (allacustrine), and a riverine group with fish exhibiting both migratory and nonmigratory behavior (fluvial migratory and nonmigratory). Noteworthy variation in movement patterns was found within lake-resident, lake–river, and river migratory groups. Migratory behavior similar to that demonstrated by each ecotype has been documented previously, but this is the first study we are aware of that has detected all three distinct, life-history-based, seasonal rainbow trout migratory ecotypes residing in the same watershed.

Seasonal Migratory Behavior

Extensive lake–river migrations of rainbow trout and cutthroat trout have been previously documented (Northcote 1969b; Burger and Gwartney 1986; Varley and Gresswell 1988; Palmer 1998), and extensive migrations have similarly been found for freshwater salmonids in fluvial environments (Northcote 1978; Schmetterling 2001). Northcote (1997) reported that lake-resident fish, while spending the majority of their life histories in lakes, may make migrations between lakes and inlet tributaries to reach suitable spawning, feeding, and refuge habitats.

We observed in this study two categories of river fish based on movement behavior: migratory and nonmigratory. Distinct migratory groups have also been demonstrated previously in rainbow trout, bull trout *Salvelinus confluentus*, and cutthroat trout (Wenger et al. 1985; Brown 1994; Swanberg 1997; Schmetterling 2001). Although we arbitrarily created two divisions, migratory and nonmigratory, within one life history type, we believe the highly diverse migratory strategies represent a continuum of fluvial rainbow trout movement behavior. The number of river nonmigratory fish (n = 10) in this study only represented a small fraction of the radio-tagged population, whereas the majority of tagged fish were migratory (n = 34). This is contrary to systems where the highly mobile fish were thought to represent the minority in freshwater salmonid populations (Hesthagen 1988; Heggenes et al. 1991).

The use of radiotelemetry has been successful in detecting long-distance movement and migrations made by rainbow trout and other stream salmonids (Wenger et al. 1985; Clapp et al. 1990; Meyers et al. 1992; Brown and Mackay 1995; Swanberg 1997; Palmer 1998; Schmetterling 2001). The extent of rainbow trout seasonal migrations in search of optimal reproductive, feeding, and overwintering habitat may be greater in watersheds with large lakes than in watersheds without lakes. Radio-tagged rainbow trout in this study moved 4–35 km to reach spawning habitat, 4–72 km to reach summer feeding habitat, and 3–60 km to reach suitable overwintering habitat. Similarly, radio-tagged rainbow trout in the Naknek River in southwest Alaska moved over 50 km to summer feeding habitat located in the northern part of Naknek Lake (Burger and Gwartney 1986). In contrast, radio-tagged rainbow trout in the Kanektok and upper King Salmon rivers in southwest Alaska, both systems without lakes, exhibited less movement when compared to rainbow trout in the Naknek and Alagnak rivers (Adams 1996, 1999).

Trophic migrations.—Trophic migrations may be common in areas where resources are widely spaced and only seasonally abundant, as well as in temperate regions where the growing season is limited (Eastman 1996). It has been suggested that the driving force of migration is food supply (Heape 1931). Rainbow trout in Alaska are known to feed upon the eggs and flesh of Pacific salmon (e.g., Russell 1977; Eastman 1996). Brink (1995) found that rainbow trout in the Gulkana River, Alaska, moved into and distributed themselves in salmon spawning habitat during the summer when chinook and sockeye salmon eggs were abundant and determined that rainbow trout spatial distribution could be predicted by salmon spawning areas. Russell (1977) noted that in lower Talarik Creek, Alaska, upstream and downstream movement of rainbow trout coincided with the upstream spawning migrations of salmon and the downstream transport of carcasses.

Chinook salmon enter the Alagnak River system in June and begin spawning activity in the middle and upper sections of the main stem during July and August (Meka, personal observation). Sockeye salmon also enter the system in June, and continue their upstream migration into the Kukaklek and Nonvianuk lakes' inlet tributaries to begin spawning activity in August and September. Chum and pink salmon (primarily even-year) enter the Alagnak River in July and begin spawning activity during August, and coho salmon enter the system in August and begin spawning activity during September and October. Results from this study support the hypothesis that movements are, at times, influenced by the migrations and spawning of salmon, based on postspawning movement patterns coinciding with salmon migrations in all three ecotypes.

Two lake–river rainbow trout captured at the Nonvianuk Lake outlet in 1997 exhibited downstream movement (47–69 km) to the braided reaches of the main stem during July, August, and September, corresponding with the arrival of chinook, chum, and pink salmon to their river spawning areas. As sockeye salmon moved farther upstream into the upper Alagnak drainage towards the end of the 1998 postspawning season, two lake–river and four lake-resident rainbow trout moved upstream (27–102 km) into the inlet tributaries, presumably in the pursuit of food. Rainbow trout sportfishing during August and September is commonly targeted at the inlet tributaries of both lakes because of the high concentration of rainbow trout feeding on the eggs and flesh of spawning sockeye salmon (Meka, personal observation).

Towards the beginning of the postspawning 1998 season, 12 river migratory fish moved downstream (5–52 km) from suspected spawning locations in the braided reaches and subsequently returned upstream to the same reaches. The subsequent upstream migrations of trout may have been influenced by the gradual increase in salmon spawning activity in the braided reaches. Eight of these fish remained in the braided reaches and eventually migrated downstream (13–52 km) to overwinter in the middle section of the main stem. Interestingly, the two lake–river fish from Nonvianuk Lake that moved downstream to the main stem were located in the same areas of the braided reaches in the upper river as the majority of river migratory fish. Even river nonmigratory rainbow trout demonstrated greater movement during the postspawning seasons of 1997 and 1998 than in other seasons, indicating that they may also move to take advantage of salmon eggs and flesh.

Overwintering migrations.—Upstream and downstream long-distance migrations to suitable winter refuge habitat have been recorded for freshwater salmonids such as cutthroat trout, rainbow trout, bull trout, and brown trout *Salmo trutta* (Wenger et al. 1985; Clapp et al. 1990; Brown and Mackay 1995; Swanberg 1997; Palmer 1998). However, even in areas with harsh winter conditions, trout may not need to make large migrations to access suitable habitat (Chisholm et al. 1987; Young 1994). Extensive movement was exhibited by lake-resident Alagnak River rainbow trout from the inlet tributaries downstream to the lake outlets (14–36 km); in contrast, some fish remained at the lake outlet and moved less than 2 km to where they overwintered. The upstream migration of trout into the upper lakes or inlet tributaries to feed on salmon eggs during the postspawning season appeared to influence the distance fish needed to travel back downstream to reach suitable overwintering habitat.

The lake–river fish that used the main stem, Nonvianuk or Kukaklek lakes, or the inlet tributaries during the postspawning seasons overwintered in their respective lakes or lake outlets. The longest detected one-way upstream movement from postspawning river habitat to lacustrine winter habitat for an individual rainbow trout in this study was 102 km. Bjornn and Mallet (1964) observed similar extensive migrations to winter refuge habitat by cutthroat trout. On average, fish that overwintered in the lakes moved more during the winter season than fish overwintering in the main stem, presumably because they traveled farther to reach their winter habitat from river or tributary summer feeding areas than fish that remained in the river.

The river migratory rainbow trout remained in the main-stem river during winter 1997–1998 and 1998–1999; the majority of fish overwintered in the lower or middle habitat zones. Downstream movement (13–52 km) from postspawning habitat in the middle or upper river sections to overwintering habitats in the lower river was the most common fall migratory behavior pattern of river fish. River nonmigratory fish overwintered in the upper, middle, lower, and tidal sections of the main stem during both winters, with the majority wintering in the heavily braided areas. Although fish within the other ecotypes made long-distance migrations to suitable overwinter habitat, river nonmigratory fish remained in the same areas throughout their tracking histories, as has been recorded by Brown and Mackay (1995).

Spawning migrations.—The spawning migrations of Yellowstone cutthroat trout have been studied extensively, and four different migratory patterns have been identified: river, river–tributary, lake–tributary, and lake–river (Varley and Gresswell 1988; Gresswell et al. 1994). Lake-dwelling rainbow trout can spawn in the inlet tributaries to lakes or in lake outlets; both types of spawning behavior may occur within a single lake (Lindsey et al. 1959; Northcote 1969a). In this study, lake-resident, lake–river, and river migratory fish made suspected spawning migrations to various types of habitat within lake outlet and river environments, indicating a strong variability in the types of habitat suitable for spawning within the Alagnak drainage.

During the spawning season, lake-resident trout either moved upstream (27–39 km) from the lake outlets to the upper lake or inlet tributaries, or remained near the outlets of either Kukaklek or Nonvianuk lakes. This indicates there may be both inlet and outlet spawners, as demonstrated in rainbow trout in the Loon Lake and Pothole Lake systems (Lindsey et al. 1959; Hartman 1969; Northcote 1969a). Varley and Gresswell (1988) reported that the rarest type of migratory spawning pattern was exhibited in populations of Yellowstone cutthroat trout, which migrated downstream to spawn. The Alagnak River lake–river fish made larger migrations during the spawning season than fish within any other ecotype. They either remained in the lakes or migrated downstream (42–60) to the main stem, or were captured in the main stem during the spawning season. We assumed the lake–river fish implanted with radio transmitters in the main stem were captured during their downstream spawning migration from Kukaklek Lake to the braided reaches because they subsequently returned upstream (66–102 km) to Kukaklek Lake during the postspawning season.

There was no migration or movement of radiotagged rainbow trout captured at Kukaklek Lake and Nonvianuk Lake outlets between drainages, indicating lake fidelity and potential reproductive isolation. However, some fish from each lake basin were located in the same braided reaches of the main stem during the suspected spawning season. Whether fish from these two major systems spawn together or whether they are distinct rainbow trout populations will depend on the outcome of molecular genetic analyses of tissue samples collected from radio-tagged rainbow trout throughout the drainage as well as other trout captured during the 1999 and 2000 spawning seasons in the braided reaches.

The literature suggests that river salmonids exhibit seasonal movement to spawning habitat (Gowan et al. 1994), although the migratory cycle between feeding, spawning, and winter habitats is not well known for river rainbow trout populations (Northcote 1997). The predominant migratory pattern of river migratory fish from this study was upstream movement to braided reaches during spawning or postspawning seasons, with subsequent return to the lower reaches of the main stem for overwintering. Many of the migratory fish that did not exhibit deliberate upstream movement during the spawning season were already located in the braided reaches during the winter and spawning seasons. The majority of river nonmigratory trout already residing in the braided reaches of the main stem made small upstream movements characteristic of spawning behavior, but on a relatively smaller scale.

Some trout may need to move only several hundred meters or less to locate suitable spawning, feeding, or winter habitats, yet they may also move great distances when resources are widely spaced (Northcote 1992). Northcote (1992) suggested that a species with both migratory and nonmigratory forms in the same watershed might have a long-term survival advantage in areas with variable resource availability and environmental conditions. Our findings imply that individual lake-resident and riverine rainbow trout can be both static and mobile, an idea that is supported by previous studies examining the patterns of movement exhibited by freshwater stream salmonids within the same system (Hesthagen 1988; Heggenes et al. 1991). Perhaps the Alagnak river nonmigratory fish and lake-resident fish that remained near Nonvianuk Lake outlet were sedentary ''residents'' that remained where food was abundant (i.e., salmon eggs) and where spawning and rearing habitats were close together (Northcote 1992). It is also possible that these fish might have exhibited long-distance migrations if they had been tracked for additional years.

Management Considerations

The three rainbow trout ecotypes in this study exhibited separate behavioral strategies throughout all seasons. The periodic, simultaneous use of the main-stem braided reaches by lake–river, river migratory, and river nonmigratory trout suggests that these areas may be critical spawning and postspawning habitat for all groups of rainbow trout, and may provide winter refuge habitat for the nonmigratory group. Because of their importance to multiple ecotypes from throughout the watershed, the braided reaches of the main stem should be considered critical habitat for Alagnak River rainbow trout.

Gresswell et al. (1994) suggested that, although little or no genetic differentiation was detected among Yellowstone cutthroat trout, documented variation of life history strategies gives a sufficient basis for managers to provide protection for each life history unit. The three ecotypes in this study have demonstrably separable behavioral strategies, because rainbow trout within each ecotype do not rigidly follow one type of spawning, feeding, or winter movement. However, because further work is needed to definitively demonstrate that the groups come from several genetically distinct populations, a conservative interim management approach would be to consider trout within each ecotype as separate population units. Further research is needed to understand the relative importance of the ecotypes and whether they are (1) true genotypes, (2) results of genetically coded but within-generation plasticity, or (3) stochastically determined. Regardless of the genotypic or phenotypic source of the ecotypes, the observed behavioral differences are linked to survival and reproduction, and are therefore valuable to preserve. Until unknowns about the sources of behavioral differences are resolved, the ecotypes of the Alagnak River, as well as those of other rainbow trout watersheds, should be considered irreplaceable and managed accordingly.

Eastman (1996) has suggested that the spatial and temporal predictability of salmon as a food resource was responsible for the evolution of migratory strategies of resident fish. We conclude that the presence of salmon spawning grounds in the Alagnak drainage determines the temporal and spatial aggregations of rainbow trout during the summer, and ultimately influences the amount of movement necessary to reach overwinter habitat from feeding habitat. The condition of rainbow trout in sockeye salmon streams has been shown to decrease during years with low salmon escapement (Ward and Larkin 1964; Russell 1977). Furthermore, Bilby et al. (1998) demonstrated the important trophic link between salmon eggs and carcasses and the density and condition of juvenile coho salmon and steelhead trout. Managers should recognize that, in systems where one or more salmon species return, rainbow trout and other freshwater fish populations that utilize salmon as a food resource may be negatively affected in years of low salmon returns or escapement (Cederholm et al. 1999).

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