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[Article]

Spawning and Movement Behavior of Migratory Coastal Cutthroat Trout on the Western Copper River Delta, Alaska

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Abstract.—We studied the movement patterns of migratory coastal cutthroat trout *Oncorhynchus clarkii clarkii* in the western Copper River delta, Alaska, near the northern extent of the subspecies' distribution. Life history information for coastal cutthroat trout is scarce within this region. Movement of coastal cutthroat trout was monitored from 1994 to 1996 with radiotelemetry and tag–recapture of fish at a two-way fishweir. Radio-tracking of 20 adults was conducted for a period ranging from 5 to 343 d. We observed anadromous and potamodromous migrations by fish that were morphologically indistinguishable and spanned a similar size range (mean fork length = 364 mm). Within these migratory groups, fish exhibited variation in movement patterns, including the timing of entry to spawning streams and postspawning movements. Anadromous and potamodromous fish entered study streams either during fall to overwinter and then spawn or during the spring just before spawning. Spawning was most concentrated in the upper portions of the study streams and occurred upstream to the highest available areas. Postspawning movements of potamodromous fish consisted of small-scale (<2 km) movement within the spawning stream or longer movements to larger rivers or lakes. Anadromous fish migrated to estuarine or marine habitat after spawning. Both anadromous and potamodromous fish moved to lentic freshwater habitat to overwinter. Our results provide empirical evidence for an array of life histories displayed by coastal cutthroat trout in south-central Alaska. We attribute the variety of movement patterns, at least in part, to the diverse assemblage of available habitat and seasonally abundant food resources provided by Pacific salmon *Oncorhynchus* spp. Future management should maintain the quality of and connectivity between reproductive, trophic, and refuge habitats distributed throughout the western Copper River delta.

Migration occurs in populations of most salmonid species in response to the spatial and temporal distribution of functional habitats necessary for feeding, overwintering, and spawning (Northcote 1997a, 1997b). The best known of these migrations are made by anadromous salmonids that can travel great distances (e.g., >1,000 km) between productive marine environments used for growth and freshwater habitats necessary for reproduction and early juvenile rearing (Gross et al. 1988). For some salmonid species, anadromy appears to be obligatory (e.g., pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta*; Groot and Margolis 1991). Other species (e.g., rainbow trout *O. mykiss* and cutthroat trout *O. clarkii*) exhibit a wide range of life histories in which some individuals or populations are anadromous and others complete their entire lives in freshwater, even in watersheds with access to the ocean (Randall et al. 1987).

Within the group of polytypic salmonid species, the life history of coastal cutthroat trout *O. clarkii clarkii* is among the most complex and flexible (Johnston and Mercer 1976; Johnston 1981; Trotter 1987, 1989). Coastal cutthroat trout range along the Pacific coast of North America from Prince William Sound, Alaska, south to the Eel River, California (Behnke 1992). Four general life histories were described by Trotter (1989), two of which correspond to life histories described by Varley and Gresswell (1988) for Yellowstone cutthroat trout *O. clarkii bouvieri*. These are (1) an anadromous form that migrates from freshwater to salt water and back again to spawn; (2) a potamodromous form that migrates between lakes and small streams (lacustrine–

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adfluvial: Varley and Gresswell 1988); (3) a potamodromous form that migrates between large rivers and smaller spawning tributaries (fluvial–adfluvial: Varley and Gresswell 1988); and (4) a resident form that completes its life cycle within its natal stream.

Management of coastal cutthroat trout populations is challenging given the variability in life history expression within the species. Multiple life history forms may coexist within the same watershed (Johnston 1981; June 1981), and individuals may change movement patterns during their lifetime (Tomasson 1978). Because sympatric individuals can be resident or migratory within a given watershed, efforts to evaluate the status of coastal cutthroat trout populations require information on seasonal movements and habitat use. Such knowledge benefits the common management concerns of determining seasonal abundance, associating fish abundance with physical habitat structure, and estimating the size and spatial extent of a population.

Despite the management challenges that these diverse movement behaviors present, coastal cutthroat trout are thought to be important indicators of the integrity of aquatic ecosystems (Behnke 1992; Reeves et al. 1993). Coastal cutthroat trout typically rear in streams for 2–5 years, after which some fish express anadromous life histories and others remain in freshwater (Trotter 1989). Due to their extended residency relative to other anadromous salmonids, coastal cutthroat trout are subject to potential impacts from land use for a longer period of their life history (Reeves et al. 1997). Although there is considerable overlap with other fishes in the lower portions of some watersheds, the freshwater distribution of coastal cutthroat trout tends to extend upstream of habitats used by other salmonids. Consequently, coastal cutthroat trout are present in a wider variety of habitats, including small headwater streams that may not be viewed as having substantial fisheries value (Rosenfeld et al. 2002).

Throughout much of the subspecies' range, coastal cutthroat trout populations have declined as a result of overharvest, negative interactions with nonnative and hatchery fishes, and habitat degradation and loss due to land management practices and flow regulation (Hall et al. 1997). Declines have been most pronounced in the southern portion of the distribution (Williams and Nelson 1997). In Alaska, limited population trend data suggest that some stocks are healthy or increasing (Schmidt 1997; Williams and Nelson 1997), but there may be regional differences in population trends within the state. For example, coastal cutthroat trout populations in portions of Prince William Sound declined after the 1988 *Exxon Valdez* oil spill (Hepler et al. 1993). In the nearby Copper River delta (hereafter "delta"), south-central Alaska, anecdotal information suggests a recent decline in coastal cutthroat trout abundance, but there is relatively little information to assess the status of most populations.

While general life history patterns for coastal cutthroat trout have been described, little is known about their specific life history and habitat requirements relative to those of other anadromous salmonids. This is especially true in the northern portion of the subspecies' range. This study was initiated to determine the movement behavior of migratory coastal cutthroat trout in the delta. The relatively pristine condition of the delta provides an excellent opportunity to examine movement patterns within an undisturbed drainage network. We used radiotelemetry to quantify movements of individual migratory fish; we also monitored movements of fish at a two-way fishweir. Our objectives were to (1) identify the common movement patterns of migratory coastal cutthroat trout and (2) contrast movement patterns of major life history types present within the study area. Results of this study are expected to aid management of coastal cutthroat trout in south-central Alaska by providing a more complete understanding of life history and migration forms in the delta.

Study Area

The delta is located on the north coast of the Gulf of Alaska, east of the town of Cordova (Figure 1). The study area is a low-lying, alluvial outwash floodplain containing numerous ponds, lakes, braided streams, and sloughs that comprise one of the largest wetlands in North America. Thilenius (1990) classified the lowland regions of the delta into several major physiographic areas, including offshore barrier sand spits and islands, ocean beaches, estuaries, old marsh, and glacial outwash piedmont. Activity of the American beaver *Castor canadensis* is prevalent throughout the delta and results in numerous on-channel ponds in the study area. The delta receives approximately 380 cm of precipitation annually, mostly in the form of rain.

This study was conducted in the western delta and focused on the drainage network surrounding Eighteen Mile Creek, including Alaganik Slough and Goose Meadows Creek (a neighboring tributary to the slough; Figure 1). Eighteen Mile Creek is a fourth-order coastal floodplain river with approximately 21 km of stream channel and a catchment area of 150 km^2. Mean stream gradient is 1%, mean discharge is estimated at 7.0 m^3/s, and mean wetted width is approximately 9 m. The substrate is dominated by alluvial gravels and cobbles. Goose Meadows Creek has physical characteristics similar to Eighteen Mile Creek. Both streams have waterfall barriers in the upper portions of their

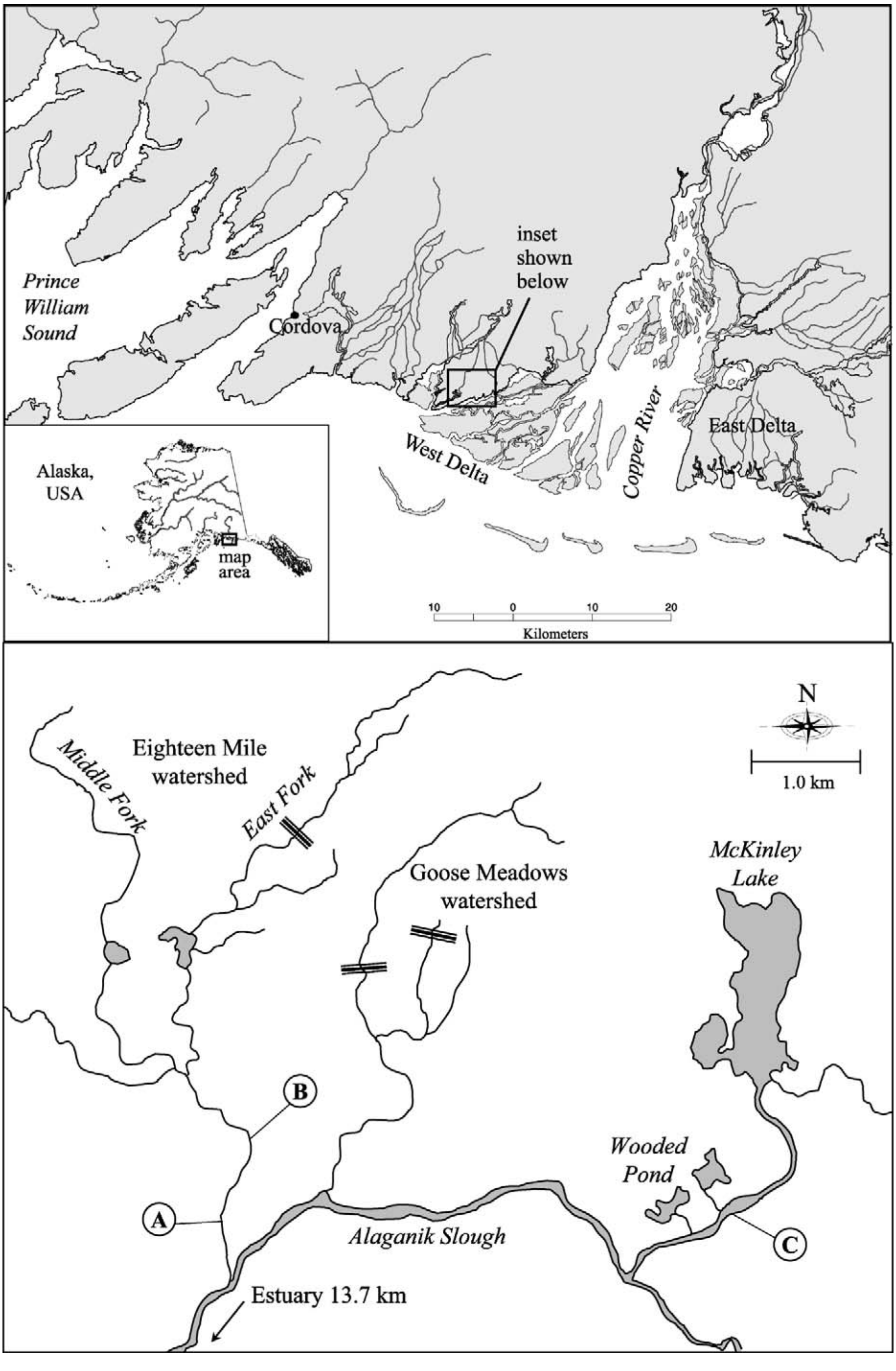

FIGURE 1.—Location of the study area and coastal cutthroat trout capture locations in the western Copper River delta, Alaska, 1994–1996 (A = Eighteen Mile Creek weir, B = angling survey at Eighteen Mile Creek, and C = angling survey at Alaganik Slough).

watersheds that limit the upstream distribution of fishes (Figure 1). Alaganik Slough is a lake outlet river that drains McKinley Lake and numerous distributary channels of the Copper River before discharging into the Gulf of Alaska. Eighteen Mile and Goose Meadows creeks enter Alaganik Slough at approximately river kilometer (rkm) 13.7 and 14.3, respectively, above the Copper River's mouth (rkm 0; Figure 1). McKinley Lake is one of the largest lakes on the western delta. It has a surface area of 114 ha, a maximum depth of 11.0 m, and a mean depth of 5.1 m. Numerous ponds and small lakes are also located within the study area, ranging in size from 324 to 4,298 m^2 and in maximum depth from 1.0 to 1.8 m. Riparian habitats are dominated by Sitka alder *Alnus sinuata* and willows *Salix* spp.; sweet gale *Myrica gale*, western hemlock *Tsuga heterophylla*, and Sitka spruce *Picea sitchensis* are minor components.

In addition to migratory coastal cutthroat trout, the study area also supports resident coastal cutthroat trout as well as populations of sockeye salmon *O. nerka*, coho salmon *O. kisutch*, pink salmon, Dolly Varden *Salvelinus malma*, threespine sticklebacks *Gasterosteus aculeatus*, slimy sculpin *Cottus cognatus*, and eulachon *Thaleichthys pacificus*.

Methods

We tagged and monitored coastal cutthroat trout with radio tags and passive integrated transponder (PIT) tags. Tagged fish were initially captured at a two-way fishweir in Eighteen Mile Creek during the spring and elsewhere by angling in the fall (Figure 1). During 1994–1996, a two-way fishweir was constructed in Eighteen Mile Creek approximately 0.8 km above the stream's mouth. The weir was constructed just after ice-out, which typically occurs during the first 2 weeks of April, and was operated through the spring until the first or second week of July. Dates of operation were 31 March–8 July 1994, 7 April–13 July 1995, and 18 April–7 July 1996. The weir was fish tight for all dates except 19–24 May 1994, when high flows breached the weir.

Upon capture, all fish were anesthetized in a buffered solution of tricaine methanesulfonate (MS-222), measured (fork length [FL], nearest mm), and weighed (g). The direction of migration (upstream or downstream) was recorded for fish captured at the weir. Fish were checked for sexual maturity and ripeness (indicated by production of milt or eggs upon gentle external massage) or for evidence of spawning (indicated by vacuous abdomens, fin abrasions, or weight loss in recaptured fish).

A sample of 250-mm FL and larger fish was opportunistically selected for radio-tagging based on fish size and availability of tags. Esophageal radio tags (Advanced Telemetry Systems, Inc., Isanti, Minnesota) were inserted through the mouth and into the stomach with a plastic straw-sized tube (Winter 1996). Radio tags had external whip antennas, weighed 5–8 g, and did not exceed 2% of fish weight (as suggested by Winter 1996). Radio tags transmitted through air or freshwater but not salt water. In 1994, radio tags were programmed to transmit for 12 h/d. Tag life ranged from 90 to 120 d. During 1994, most radio tags were pulled from fish that returned downstream to the Eighteen Mile Creek weir because the tags were expected to expire shortly thereafter. In 1995 and 1996, tags with variable duty cycles were used to prolong battery life. These radio tags were programmed to transmit for 4–6 h/d on each day during spring, 1–4 d/week during summer and fall, and 1 week/month during winter. The maximum expected life span for these tags was 12–13 months, although the observed tag life was variable.

During the study, 25 coastal cutthroat trout were implanted with radio transmitters. Four fish were tagged in 1994, 7 fish were tagged in 1995, and 14 fish were tagged in 1996. Of the 25 radio-tagged coastal cutthroat trout, 5 experienced tag failure or were depredated before any movement data could be collected; these fish were excluded from further analysis. Of the remaining 20 fish, 1 fish did not spawn and 1 fish was depredated before postspawning movement data could be collected. Five fish were tracked through fall and winter.

In 1995 and 1996, non-radio-tagged coastal cutthroat trout moving upstream past the weir were implanted with individually coded PIT tags. Tags were inserted into the body cavity with a sterilized 12-gauge hypodermic needle. Fish tagged with either radio transmitters or PIT tags were held for 24 h and checked for tag retention or handling injury before being released at the site of capture. All fish captured at the weir were checked for PIT tags with a handheld tag detector and were visually checked for radio tags.

Radio-tagged fish were located from the ground with a handheld, two- or three-element Yagi antenna. Attempts to relocate fish began 24 h after release via foot, car, airboat, or a combination thereof (hereafter referred to as ground surveys). The frequency of ground surveys varied according to tag duty cycle, season, and weather conditions. Ground surveys were conducted daily during spring and weekly during summer and fall. In addition to ground surveys, aerial surveys were conducted from 1 to 7 d/week in summer to determine the timing of postspawning and seaward migrations of anadromous fish. Weekly flights were made throughout the late summer and early fall to determine timing of reentry of anadromous fish into freshwater. During the winter, either ground or aerial surveys were made once or twice monthly.

During the spawning period, spawning was confirmed for five fish through direct observation (e.g., fish observed digging redds) and for eight fish by examination of fish condition (e.g., weight loss, vacuous abdomen, fin abrasions) upon recapture at the weir. Spawning was assumed to have occurred for five fish that migrated to areas where other fish were observed spawning.

During ground surveys, fish locations were determined to the nearest meter with triangulation methods and were recorded on aerial photographs (1 cm = 0.2 km). Distances between fish locations were measured with a map wheel. Unless directly observed, the date of an event (e.g., entry from freshwater into salt water) was interpreted as the average date between contacts (Swanberg 1997).

To categorize movement patterns, we created individual movement plots to graphically depict watershed locations (rkm measured from the mouth of Eighteen Mile Creek) of each fish over time. Because of the small sample size of radio-tagged fish, we pooled observations across years after examination of individual movement plots revealed that the diversity of movement patterns we observed were represented during each year of the study.

To further categorize movement patterns, we subjected the data to an agglomerative hierarchical clustering analysis that used the unweighted pair–group method with arithmetic averages (Sneath and Sokal 1973). Cluster analysis was conducted in Statistical Analysis System software (SAS Institute 2003). Because relocation data were limited for the fall and winter seasons, we restricted statistical analysis to include only spawning and postspawning movement patterns for the 18 confirmed spawners that had a minimum of two relocations during the postspawning period. The data used in the cluster analysis included spawning location (rkm above the estuary), postspawning distance moved (km traveled from spawning location), and a categorical variable indicating whether fish were summer residents within their spawning stream. Median spawning locations were assigned for three confirmed spawners whose exact spawning locations were unknown. Spawning was confirmed for these fish by examination of fish condition upon recapture at the weir. The categorical variable was included in the analysis because the final summer destination of some fish emigrating from Eighteen Mile Creek was unknown due to tag removal or tag failure after at least two postspawning relocations. For these fish, a minimum postspawning distance moved was

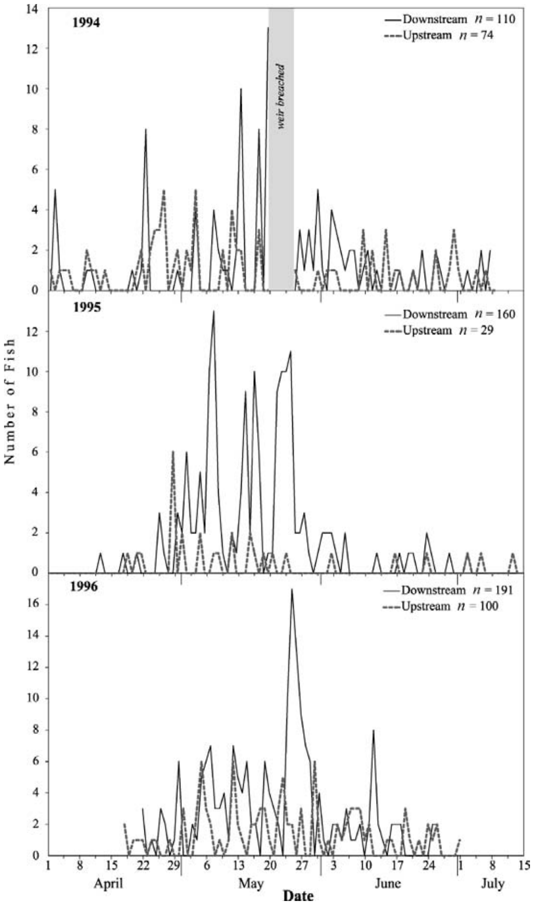

FIGURE 2.—Numbers of coastal cutthroat trout moving upstream or downstream past a fishweir in Eighteen Mile Creek, Alaska, during spring 1994–1996.

used in the analysis based on the position of the final relocation for each individual.

To test for differences in fish size and migration timing among groups of fish, the date of entry (Julian date) into spawning streams and lengths of fish exhibiting different movement patterns were compared by use of Student's t-test ($\alpha = 0.05$).

Results

Annual counts of coastal cutthroat trout moving upstream past the Eighteen Mile Creek weir ranged from 29 to 120 fish (Figure 2). Spring immigration into Eighteen Mile Creek occurred as early as 1 April and as late as 14 June (Figure 2). Radio-tagged fish represented 5–24% of the total number of coastal cutthroat trout moving upstream past the weir during each year. Lengths of radio-tagged fish at initial capture averaged 364 mm FL (SD = 45 mm; range =

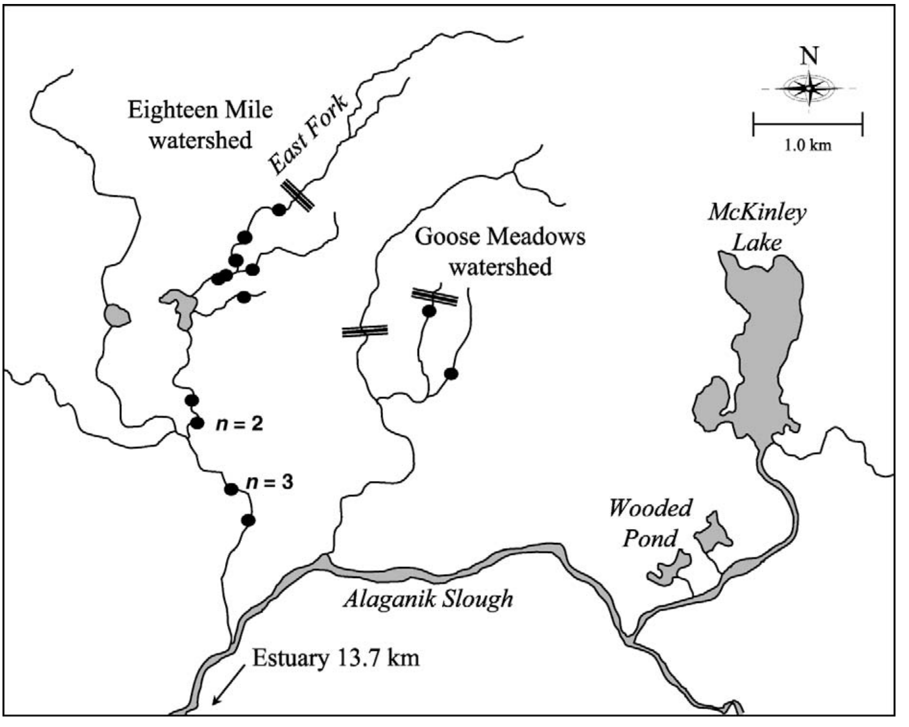

FIGURE 3.—Map of spawning locations (filled circles) of radio-tagged coastal cutthroat trout in the Copper River delta, Alaska, 1994–1996. Bars indicate fish passage barriers.

272–489 mm), and weights averaged 498 g (SD = 219 g; range = 188–1,197 g).

Radio-tagged coastal cutthroat trout moved an average of 3.1 km (SD = 1.3 km; range = 1.2–4.8 km) above the mouth of Eighteen Mile Creek at an average rate of 0.5 km/d. Spawning occurred in the most upstream available areas, where either barriers or low streamflows prohibited further movement (Figure 3). Fish reached their spawning locations an average of 7 d (SD = 5 d; range = 1–19 d) after passing through the weir. Most radio-tagged fish moved directly to spawning habitats. Four fish showed exceptions to this pattern, spending from 4 to 13 d in large pools associated with beaver dams before moving to their spawning locations (Figure 4).

Once they reached their spawning locations, radio-tagged fish remained within a 100-m reach during the spawning period, which typically lasted 3 d or less. Five females (283–363 mm FL) were directly observed spawning; these fish paired with males ranging from 130 to 270 mm FL. Females constructed redds in the tails of pool habitats, while dominant males near redds defended territories from two to three 100–130-mm males. Smaller males were cryptically marked with dense spotting and dark coloration.

Cluster analysis and visual examination of movement plots of radio-tagged fish identified anadromous and potamodromous movements as the two major migration types (Figure 5). Fish length was not significantly different between anadromous and potamodromous groups (*t*-test: $P = 0.69$; Table 1). The two groups also had similar dates of entry into Eighteen Mile Creek (*t*-test: $P = 0.66$).

Within the anadromous grouping, fish were further subdivided by spawning location (rkm above estuary). Anadromous fish spawned in Eighteen Mile and Goose Meadows creeks at an average distance of 16.7 km (SD = 0.9 km; range = 14.7–17.3 km) above the estuary (Table 1). The only major subdivision within this group occurred between three fish that spawned in upper stream reaches and one fish that spawned in the lower 2 km of Eighteen Mile Creek (fish 23 in Figure 5).

After spawning, anadromous fish emigrated from their spawning locations at an average rate of 1.6 km/d (SD = 1.52 km/d; range = 0.6–4.3 km/d) and entered the estuary between 17 May and 15 June. Movements within the estuary could not be determined because radio tags could not transmit through salt water, but all fish were relocated during the fall after returning to freshwater. Anadromous fish returned between 2 and

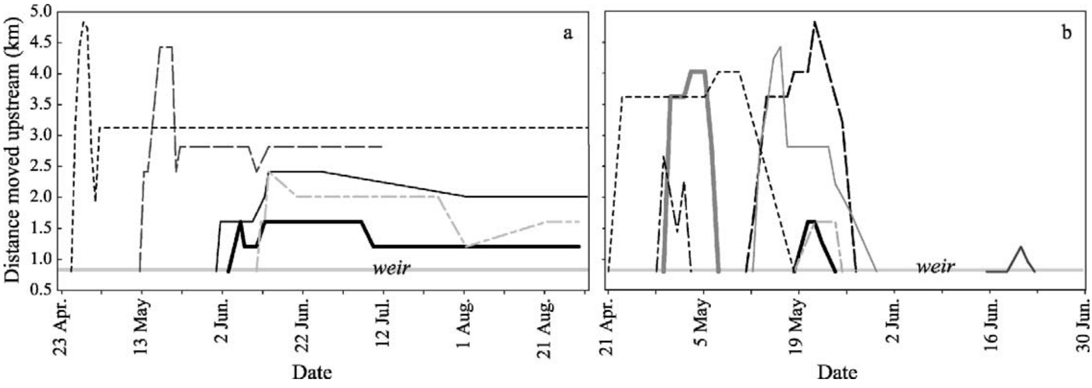

FIGURE 4.—Distances moved (km) upstream of the mouth of Eighteen Mile Creek, Alaska, relative to calendar date in 1994–1996 for radio-tagged coastal cutthroat trout that **(a)** remained in the creek after spawning or **(b)** returned to a fishweir in the creek after spawning. Each line represents an individual fish.

27 August after spending an average of 71 d (SD = 11 d; range = 48–93 d) in estuarine or marine habitat.

Potamodromous fish exhibited greater diversity in movement patterns than anadromous fish and were divided into two distinct subgroups: (1) fish that established summer residency within the spawning stream (Eighteen Mile Creek) and (2) fish that emigrated from the spawning stream to other freshwater habitats immediately after spawning (Figure 5). Fish length was not significantly different between the two potamodromous migratory groups (t-test: $P = 0.21$). The two groups also had similar dates of entry into Eighteen Mile Creek (t-test: $P = 0.34$).

Fish in the first potamodromous group ($n = 6$) were characterized by small-scale (<2 km) downstream movement within Eighteen Mile Creek. Fish moved an average of 0.9 km (SD = 0.7 km; range = 0–1.6 km) downstream from their spawning locations (Figure 4). Fish in the first group were further characterized by spawning location and clustered into subgroups that spawned above and below beaver ponds in Eighteen Mile Creek. Postspawning movements within this group were less direct than prespawning movements, consisting of periodic small-scale movements between large pools associated with beaver dams (Figure 4).

The first potamodromous movement pattern observed in radio-tagged fish was also exhibited by some of the PIT-tagged fish initially captured at the Eighteen Mile Creek weir. In 1995, 22 of 28 (79%) PIT-tagged upstream migrants had not returned to the weir before it was removed on 13 July. In 1996, 58 of 76 (76%) PIT-tagged fish had not returned to the weir before it was removed on 7 July. The proportions that experienced mortality, emigrated after weir removal, or established

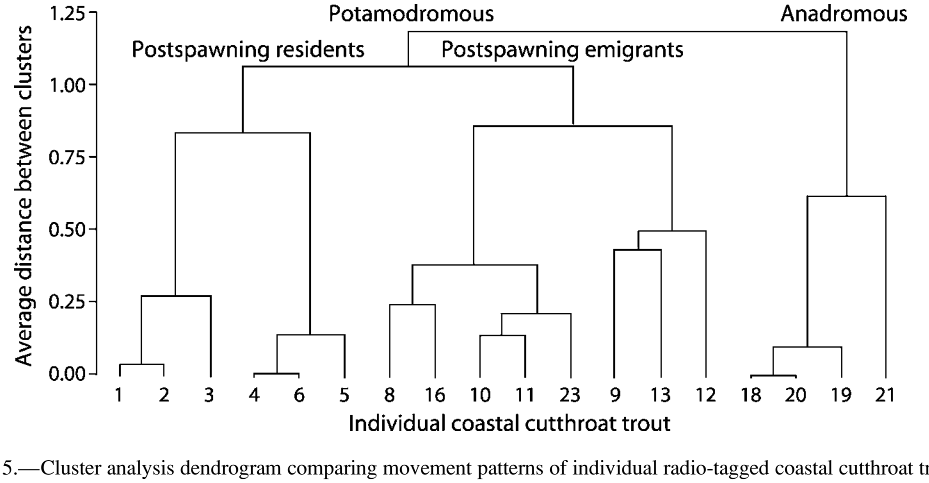

FIGURE 5.—Cluster analysis dendrogram comparing movement patterns of individual radio-tagged coastal cutthroat trout (fish numbers 1–23) in the Copper River delta, Alaska, during 1994–1996.

TABLE 1.—Sample size and mean (SD) date of entry into spawning streams, FL (mm), spawning location (rkm above estuary), and postspawning distance moved within freshwater (km) for three movement types of radio-tagged coastal cutthroat trout in the Copper River delta, Alaska, 1994–1996.

Movement type	*n*	Mean entry date	Mean FL	Mean spawning location	Mean postspawn distance moved
Potamodromous 1	6	16 May	339 (33)	17.0 (1.4)	1.2 (0.6)
Potamodromous 2	8	3 May	360 (28)	17.0 (1.3)	5.8 (3.5)
Anadromous	4	14 May	362 (91)	16.7 (0.9)	16.7 (0.9)

residency in Eighteen Mile Creek are not known. However, the rate of return to the weir was much lower than that expected based on mortality alone (mortality of radio-tagged fish was 18%). If movements of PIT-tagged fish were similar to those of radio-tagged fish, then we would not expect emigration after weir removal because radio-tagged fish that did not return to the weir by 1 July remained in Eighteen Mile Creek through the summer (Figure 4).

The second potamodromous group consisted of radio-tagged fish that returned to the weir after entering Eighteen Mile Creek during the spawning period. These fish ($n = 8$) returned to the weir between 3 May and 22 June after spending an average of 13 d (SD = 8 d; range = 6–28 d) in Eighteen Mile Creek. Similar to the first potamodromous group, fish in the second group were further characterized by spawning location and clustered into subgroups that spawned above and below beaver ponds in Eighteen Mile Creek. Fish returning to the weir exhibited signs of spawning, such as abraded caudal fins and vacuous abdomens, and lost an average of 13% of their body weight (SD = 4%; range = 8–20%). Postspawning movements of emigrating fish were generally direct and occurred at a rate of 0.6 km/d (SD = 0.46 km/d; range = 0.20–1.60 km/d). In all but two cases, fish progressed downstream at successive postspawning relocations (Figure 5). Within the group of emigrating fish, the analysis further clustered individuals by the postspawning distance moved.

The second potamodromous movement pattern of radio-tagged fish was also observed in some of the PIT-tagged fish initially captured at the Eighteen Mile Creek weir. Downstream weir captures of coastal cutthroat trout ranged from 93 to 240 fish (Figure 2) and included some of the fish that had been captured and tagged while moving upstream past the weir. In 1995, 6 of 28 (21%) PIT-tagged upstream migrants returned to the weir after spending an average of 12 d (SD = 26 d; range = 1–67 d) in Eighteen Mile Creek. In 1996, 18 of 76 (24%) PIT-tagged upstream migrants returned to the weir after spending an average of 6 d (SD = 9 d; range = 1–35 d) in Eighteen Mile Creek. However, the proportion of PIT-tagged fish returning to the weir that subsequently underwent potamodromous or anadromous migrations is unknown.

Although our sample size of radio-tagged fish tracked during the winter is too small for statistical analysis, observations of five fish provided information on migrations to winter habitat. All five fish moved to ponds or lakes on the delta, reaching their winter locations between 26 September and 14 November. One fish returned to a pond located on the Middle Fork of Eighteen Mile Creek after spending the summer in estuarine or marine habitat. The remaining four fish were tracked from summer locations in freshwater habitat to their winter locations. Freshwater migrations occurred at an average rate of 0.6 km/d (range = 0.1–1.9 km/d), and fish moved an average of 6.8 km (SD = 4.85 km; range = 1.2–9.6 km) to reach winter habitat. The radio tags of two fish expired during the winter. Two fish remained in their winter locations for 194 and 179 d before migrating to Eighteen Mile Creek to spawn during the spring. One fish remained in McKinley Lake (its overwintering site) and was tracked as moving within the lake throughout the spring and summer until the radio tag expired on 6 September (total tracking period = 310 d).

Discussion

This study provides several insights into the life history of coastal cutthroat trout in the northern portion of the subspecies' distribution, where such information was previously lacking. We observed both anadromous and potamodromous migrations by fish that spawned within Eighteen Mile Creek. Potamodromous fish exhibited greater diversity in movement patterns than anadromous fish and were divided into two distinct subgroups: (1) fish that established summer residency within the pawning stream after small-scale (<2 km) downstream movements and (2) fish that emigrated from the spawning stream to other freshwater habitats immediately after spawning.

Results from our study generally correspond to anadromous and potamodromous migratory patterns reported for coastal cutthroat trout in other areas (reviewed in Trotter 1989, 1997), but few studies have documented the range of movement patterns we observed for migratory fish with access to marine habitats. Tomasson (1978) identified sympatric potamodromous and anadromous coastal cutthroat trout populations from the Rogue River, Oregon, by analyzing the chemical composition of fish scales. Similarly, Johnson et al. (1999) reported sympatric potamodromous and anadromous coastal cutthroat trout occurring in the Umpqua River, Oregon. However, elsewhere (e.g., Willamette River, Oregon: Moring et al. 1986), potamodromous migrations are typically associated with populations existing above barriers that restrict anadromous migration (Johnson et al. 1999). Before our study, migratory coastal cutthroat trout in the delta were assumed to be anadromous because they are relatively large (>300 mm FL), live near salt water, and undergo seasonal migrations. We observed that radio-tagged fish exhibiting different movement behaviors were morphologically indistinguishable and spanned a similar size range. While the co-occurrence of potamodromous and anadromous fish may be unique to certain watersheds, the difficulty in distinguishing among life history forms may mean that the phenomenon is more prevalent than previous reports suggest.

Fish of different migratory forms exhibited temporal overlap and possibly spatial overlap on the spawning grounds, although the spatial resolution of fish relocations was not sufficient to identify selective mating of fish. Our direct observations of five radio-tagged spawners indicate that migratory coastal cutthroat trout, including anadromous fish, may interbreed with smaller resident forms. These results are consistent with reports of larger migratory female coastal cutthroat trout associating with small, “cryptically colored” males during spawning periods (Northcote 1997b). June (1981) documented sympatric rearing and spawning between anadromous and resident forms of coastal cutthroat trout. Similarly, Jones (1976) suggested that offspring from resident or potamodromous coastal cutthroat trout contributed significantly to anadromous runs. However, others have found within-basin genetic divergence of coastal cutthroat trout exhibiting different life histories (Zimmerman et al. 1997), which suggests assortative breeding among ecotypes. Two alternative explanations for this phenomenon were presented by Johnson et al. (1999): (1) some coastal cutthroat trout in migratory populations may mature as precocious male parr and thus do not undertake extensive migrations and (2) coastal cutthroat trout of one life history form may readily interbreed with those of other life history forms. Additional genetic studies will be necessary to determine the extent to which fish exhibiting different movement patterns in the delta constitute distinct genotypes.

The range of postspawning migration patterns we observed may be explained, in part, by movement of coastal cutthroat trout to exploit a diversity of food resources associated with the seasonal abundances of other salmonids. Other studies have demonstrated that movements of potamodromous salmonids are related to the upstream spawning migrations of Pacific salmon and the subsequent downstream transport of carcasses (Russell 1977; Brink 1995; Meka et al. 2003). Meka et al. (2003) found that the variety of seasonal movement patterns exhibited by migratory rainbow trout was greatest during the postspawning period in the Alagnak River, Alaska, and suggested that this increase in movement activity was a response to food resources supplied by the presence of spawning salmon.

Similar to the results of Meka et al. (2003), we found that radio-tagged coastal cutthroat trout were present in the widest variety of habitats (including lotic and lentic freshwater habitats and estuarine and marine habitats) during summer, the primary season of salmonid spawning and juvenile migration. Sockeye salmon enter the Alaganik River in June and spawn in McKinley Lake and its tributaries in July and August. Coho salmon enter the Alaganik River system in August and begin spawning activity in Eighteen Mile Creek and other tributaries during September and October. By means of underwater videography, observations were made of coastal cutthroat trout feeding upon coho salmon eggs in Eighteen Mile Creek (U.S. Forest Service, Cordova Ranger District, unpublished data). Additionally, migratory coastal cutthroat trout are known to prey on juvenile salmonids (Trotter 1997). We observed radio-tagged coastal cutthroat trout feeding on coho salmon smolts in Eighteen Mile Creek during the spring. The out-migration of coho salmon and sockeye salmon smolts from the study streams provides an abundant prey source for migratory coastal cutthroat trout during the postspawning period. Therefore, we speculate that the seasonal abundance of prey within the study area allows relatively large migratory coastal cutthroat trout to meet their trophic needs without migrating to marine habitats.

Our study focused on spawning and postspawning movement patterns of radio-tagged coastal cutthroat trout, but observations of a smaller number of radio-tagged fish tracked outside of this period and captures made at the Eighteen Mile Creek weir provide insight into the timing of freshwater entry of anadromous fish. Our results suggest that migratory coastal cutthroat trout in the delta enter spawning streams during fall and spring. The presence of sea lice *Lepeophtheirus salmonis* on some fish captured at the weir during spring indicated the recent transit of fish through salt water before migration to Eighteen Mile Creek (Hahnenkamp and Fyhn 1985). Fall entry was exhibited by one anadromous radio-tagged fish that wintered in an on-channel beaver pond in Eighteen Mile Creek after spending the summer in estuarine or marine habitat. Fall entry into freshwater (but not Eighteen Mile Creek per se) was also observed for three other anadromous radio-tagged fish. Other large migratory coastal cutthroat trout that were not captured while moving upstream past the weir were first captured in the early spring upon emigration from Eighteen Mile Creek; this suggests entry into the system before spring, most likely during the previous fall.

The bimodal pattern of stream entry is similar to migration patterns for other populations of coastal cutthroat trout in northern portions of the distributional range (Jones 1976; Jones and Seifert 1997) but differs from those reported for southern populations. In the more southerly portions of their range, coastal cutthroat trout typically return to natal streams in fall to overwinter and then spawn, and spring migrations have not been frequently documented (Trotter 1987, 1997). Although factors such as food availability and hydrology can also explain some movement patterns (Johnston 1981), the redistribution of fish from overwintering to natal watersheds may account for the bimodal pattern of stream entry we observed. Coastal cutthroat trout are thought to exhibit high fidelity to spawning locations (Trotter 1997), although they may overwinter in watersheds other than their natal streams (Jones and Seifert 1997). The higher prevalence of lakes in the northern portion of the subspecies' range may provide winter habitat in smaller neighboring watersheds that are otherwise lacking in deep winter refuges for migratory coastal cutthroat trout. For example, in southeast Alaska, Jones and Seifert (1997) described saltwater migrations of coastal cutthroat trout from large mixed-stock overwintering congregations in Lake Eva and Auke Lake to 27 different coastal spawning streams during the spring. In their study, many coastal cutthroat trout migrated to very small coastal streams to spawn, while others remained in their overwintering systems for spawning. Similarly, Johnston and Mercer (1976) described two distinct migration periods for anadromous coastal cutthroat trout in coastal Washington streams: (1) late freshwater entry in winter or spring and (2) early freshwater entry starting in August and followed by overwintering in spawning streams. Early-entry stocks were associated with larger streams ($\geq$1.4 m^3/s), and late-entry stocks were found in smaller streams ($<$0.6 m^3/s) that flowed directly into salt water (Johnston and Mercer 1976).

In our study, all radio-tagged coastal cutthroat trout that were tracked during the fall and winter periods migrated to lentic freshwater habitats. Radio-tagged fish overwintered in McKinley Lake, one of the largest lakes on the west Copper River delta, and both anadromous and potamodromous fish also used smaller beaver ponds during winter. These smaller ponds are not expected to support large congregations of fish during winter, but because they are numerous and widespread they may be as important as larger lakes for providing winter habitat. Movement to deep, slow-water areas is consistent with patterns observed for coastal cutthroat trout in southeast Alaska (Armstrong 1971; Jones and Seifert 1997) and is similar to behavior reported for interior cutthroat trout subspecies (e.g., Brown and Mackay 1995; Colyer et al. 2005).

Northcote (1984) observed that migratory behavior arises from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction. In reviewing the life history of coastal cutthroat trout, Northcote (1997b) found that fish behavior fit a functional model depicting movements as a cycle of migrations (trophic, refuge, and, eventually, reproductive) among three critical habitats (feeding, wintering, and spawning) and that the geographic arrangement and proximity of critical habitats determine the extent of seasonal movements. Northcote (1997b) also suggested that the variability and plasticity in coastal cutthroat trout movement patterns are responses to the dramatically changing landscape and climate in which the subspecies evolved. We suggest that expression of movement pattern variability also depends on the template (sensu Southwood 1977) provided by contemporary landscape conditions on the delta. Equally important to life history expression in the delta may be the presence of a highly diverse and relatively pristine assemblage of freshwater habitat types that makes multiple migratory strategies successful. Other researchers have noted a relationship between habitat integrity and diversity of life history expression. For example, Gresswell et al. (1997) found that habitat diversity in the relatively pristine tributary drainages of Yellowstone Lake contributed to the expression of variation in cutthroat trout life history traits, including movement patterns. If the presence of multiple migratory strategies enables long-term population resiliency (Stearns 1976), then the persistence of migratory coastal cutthroat trout will require maintenance and connectivity of the critical habitat types located sometimes disparately across the delta.

Our results agree with those of other studies (e.g., Gowan et al. 1994; Hilderbrand and Kershner 2000; Colyer et al. 2005) suggesting that salmonid movements occur more frequently and are more complex than is commonly recognized. We provide empirical evidence for an array of life histories displayed by coastal cutthroat trout near the northern extent of their distribution. Increased awareness of migratory behavior should aid in the management of coastal cutthroat trout in south-central Alaska. Future management of this subspecies in the delta will need to consider the presence of mature fish in a wide variety of freshwater habitats throughout the year. Our observations suggest that the viability of alternative movement strategies for coastal cutthroat trout may rely on the seasonal prey abundance provided by healthy populations of Pacific salmon. Although the spectrum of migratory strategies displayed by coastal cutthroat trout poses a challenge to management, land use practices that facilitate behavioral flexibility by maintaining connectivity between critical habitat types should enable the long-term persistence of this species.

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