Seaward Migration of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* from Four Tributaries of the Columbia River

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Abstract.—Timing and speed of juvenile coastal cutthroat trout *Oncorhynchus clarkii clarkii* migration was investigated using both active and passive radio and acoustic telemetry in the spring of 2002 and 2003. Actively migrating cutthroat trout in Germany, Abernathy, and Mill creeks and the Chinook River (tributaries of the lower Columbia River: river km 91, 88, 87, and 6, respectively) were captured by screw trap, implanted with either a radio transmitter or acoustic pinger, and monitored. The data suggest that migrant cutthroat trout leave the tributaries and make rapid, directed movements into seawater, often within five days of entry into the main stem environment. In the spring of 2003, the telemetry effort emphasized active tracking to gather specific high resolution movement data on cutthroat trout leaving the three creeks. Directed downstream movement was correlated with outgoing tidal flows and was greatest just after dawn and dusk. Because of life history similarities, anthropogenic activities and management actions in the main stem Columbia River that influence salmon smolts are likely to affect anadromous coastal cutthroat trout smolts in a parallel fashion.

Coastal cutthroat trout *Oncorhynchus clarkii clarkii* are found on the West Coast of North America from Alaska to northern California (Behnke, 1992; Gerstung 1997; Schmidt 1997). These fish exhibit tremendous diversity in life history strategies both within a watershed and throughout their range (Armstrong 1971; Giger 1972; Jones 1978; Johnston 1982; Trotter 1989; Northcote1997). Some individuals complete their life history within their natal stream yet sympatric individuals may undertake active downstream migrations (June 1981; Johnston 1982; Northcote 1997).

There are no clear morphological distinctions between juvenile cutthroat trout that are resident or migratory (Tomasson 1978; Fuss 1982). Migratory cutthroat trout generally emigrate from natal waters at age 2 or 3 in the spring (Giger 1972; Sumner 1972; Trotter 1989). Age 2 migrants predominate in the lower Columbia River watershed of Oregon and Washington (Johnston 1982; Trotter 1989). Seaward migration at the juvenile stage affords periods of high growth in the ocean environment (Gross 1988). This migration also requires the development and maintenance of appropriate osmotic tolerances necessary for survival.

Migratory cutthroat trout have been characterized as weakly anadromous (Northcote 1997) and reportedly select lower salinities in the estuary (Loch and Miller 1988). While cutthroat trout have been caught offshore, conventional wisdom prescribes that migrating cutthroat trout do not venture far from the estuary if at all (Tipping 1981; Pearcy 1997). In many systems, these trout are thought to make more extensive use of the main stem river and estuary habitats (as both juveniles and adults) rather than offshore environments. Though migrating juveniles are characterized as "smolts" (Trotter 1997), it is unclear whether juveniles undergo a parr-smolt transformation process similar to those observed in other salmonids (Hoar 1976; McCormick and Saunders 1987). Shifts in migratory behavior and physiology (e.g., elevated gill Na^+,K^+-ATPase activity) associated with smolting are not well documented in coastal cutthroat trout.

Many migratory populations of coastal cutthroat trout have declined in recent years, including those of the Columbia River (Nehlsen et al. 1991; Hooton 1997; Leider 1997). Coastal cutthroat trout have been impacted by anthropogenic practices such as logging (Holtby 1987; Johnson et al. 1999) over fishing (Giger 1972; Ricker 1981; Gresswell and Harding 1997), and artificial propagation (Campton and Utter 1987; Flagg et al. 1995). In addition, coastal cutthroat trout are thought to use estuaries more extensively than other Pacific salmonids, particularly during certain stages in their life history. This may make them more vulnerable to changes in estuarine conditions than other Pacific salmonids (Giger 1972; Pearcy 1997).

The objective of this study was to determine the movement patterns of coastal cutthroat trout entering the Columbia River from four tributaries known to have migratory populations and to characterize the degree to which these fish used the main stem and estuary of the Columbia River. Additionally, gill biopsies of study fish were used to measure Na^+,K^+-ATPase activity as an indirect indicator of smolt development.

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Methods

Study area.—Cutthroat trout from four tributaries to the Columbia River, Germany Creek (river kilometer [rkm] 91), Abernathy Creek (rkm 88), Mill Creek (rkm 87) and the Chinook River (rkm 6), were studied in 2002 and 2003 using radio and acoustic telemetry (Figure 1). The Chinook River is a tidal system that is regulated by a tide gate at its confluence with the Columbia River. This system experiences salinity fluctuations from 0 ppt to full strength seawater and empties into an estuarine mixing zone. Germany, Mill, and Abernathy creeks are third order systems that experience tidal fluctuations at their confluences with the Columbia River, but do not experience salinity fluctuations.

Capture of cutthroat trout.—In 2002 and 2003, juvenile cutthroat trout were captured at the mouths of Germany, Abernathy, and Mill creeks in 1.5 m screw traps (operated by the Washington Department of Fish and Wildlife [WDFW]) and in a screw trap (2.4 m) at the mouth of the Chinook River (operated by Sea Resources, Incorporated, Chinook, Washington). In 2002, cutthroat trout implanted with radio tags were captured from May 5 through May 30, while those implanted with acoustic tags were captured from May 12 through May 21. In 2003, cutthroat trout receiving radio tags were captured from May 9 to June 25, while those receiving acoustic tags were captured from May 17 through June 11. Water temperature ranges observed during tagging are shown in Table 1.

Tagging.—Fish were held in the screw traps a maximum of 24 h prior to tagging. Cutthroat trout were anesthetized with a buffered solution of MS-222 (100 mg·l^{-1}, NaCO$_3$ buffered 0.2 mmol NaHCO$_3$, pH = 7.0) in 4 L of water from the area of capture, then measured for length and weight. Also, a non-lethal gill biopsy taken for subsequent analysis of Na$^+$,K$^+$-ATPase activity. Two to four filaments from the first gill arch on the left side were removed with iris scissors above the septum (which avoids major vascularization) and handled as described below. Fish were then implanted with an acoustic (Vemco V8SC-6L-R256 coded pingers; 26 mm x 9 mm diameter; 3.1 g; 69 kHz, 20-60 sec pulse rate; estimated minimum tag life of 68 d) or radio (Lotek Nano-tags NTC-4-2S; 1.65 g; 148-150 MHz; 3 sec pulse rate; estimated minimum life of 25 d) tag.

Fish larger than 37 g were selected for implantation of acoustic tags (this excluded less than 10% of collected fish). The skin on the ventral surface was swabbed with Betadine (10% povidone-iodine) and an incision made in the peritoneal wall with a sterilized scalpel tip. The tag was inserted through the incision which was then closed with three sutures (Coated Vicryl 5-0 braided absorbable suture) and swabbed with Betadine. Typically the wound heals within 7-10 d (depending on temperature) and sutures dissolve within 10-14 d (Zydlewski, unpublished data).

Fish greater than 30 g were selected for radio tagging (excluding only a few fish). Radio tags were inserted into the peritoneal cavity in the same fashion as acoustic tags
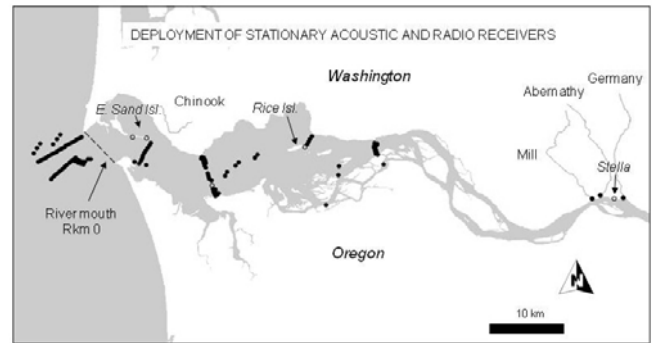

FIGURE 1.—Deployment of stationary acoustic (solid circle) and radio receivers (open circle) in the Columbia River in 2003. The four tributaries studied (Germany Creek, Mill Creek, Abernathy Creek, and Chinook River) are indicated.

TABLE 1.—Mean fork lengths (cm), weights (g), and condition factors (100 • g • cm^{-3}) of coastal cutthroat trout implanted with acoustic and radio tags in 2002 and 2003. Values are presented ± 1SD. There are no statistical differences between groups. Ranges of water temperatures at collections for each tag type within each year are given.

Year	Tag type	River (n)	Length (cm)	Weight (g)	CF (100 •g •cm^{-3})
2002	Acoustic	GERM (1)	20.4	72.2	0.85
	(9-11 °C)	ABER (12)	19.2±1.4	62.0±15.7	0.86±0.04
		MILL (10)	18.7±1.3	55.5±12.5	0.83±0.04
		CHIN (26)	20.0±2.7	72.8±33.3	0.86±0.06
	Radio	GERM (21)	18.8±1.5	60.6±15.8	0.89±0.06
	(7-12 °C)	ABER (32)	18.8±2.1	61.4±22.3	0.89±0.06
		MILL (43)	18.4±1.4	53.7±13.2	0.85±0.06
2003	Acoustic	GERM (15)	17.9±0.9	48.4±7.1	0.84±0.05
	(7-15 °C)	ABER (9)	18.4±1.0	56.8±12.3	0.91±0.08
		MILL (15)	19.4±1.6	66.6±16.9	0.90±0.09
	Radio	GERM (8)	18.5±1.6	56.1±13.5	0.87±0.06
	(13-18 °C)	ABER (4)	17.3±1.2	43.4±10.1	0.83±0.05
		MILL (10)	18.5±1.2	56.8±13.0	0.85±0.07
		ALL (206)	18.8±1.8	59.4+19.6	0.87+0.06

except for accommodation of an external antenna which was threaded through the body cavity with a sterile 18 gauge, 20 cm long deflected septum needle. The needle was then pushed through the lateral wall of the cavity approximately 1 cm anterior to the anus on the right side. The area around the antenna exit was swabbed with Betadine and the initial incision closed with two sutures. Cutthroat trout receiving either tag were allowed to recover for 10-15 min prior to release downstream of the trapping sites (within 50 m) at the closest area away from rapid flow.

Radio tracking.—In 2002 and 2003, movements of tagged fish were monitored passively via five stationary radio telemetry locations. The locations of the receivers (Lotek SRX-400 receiver/dataloggers; as indicated on Figure 1 for 2003) varied slightly between years; however areas of coverage were consistent. Receivers were located at Stella (Washington), Rice Island, and East Sand Island, and Astoria Bridge. These units were equipped with yagi antenna oriented towards the main channel of the Columbia River and were downloaded multiple times through the study. Observations were considered to be duplicates if occurring at the same point within a 10 min interval. The time of duplicate observations were averaged for analysis.

In both 2002 and 2003, active tracking was performed by both boat (minor component in 2002) and automobile. The areas of initial capture and release were generally checked at 24 h intervals to determine if individuals remained near the tag and release site. In 2003, greater emphasis was put on active tracking by boat. Subsequent to tagging, an individual observed leaving the tributary was generally tracked until it could not be relocated. Location of tagged fish was determined using two boat-mounted yagi antennas and a hand-held yagi antenna with Lotek SRX-400 receivers. Tests with drones verified the ability to confidently localize tag positions to within 50 m. Twenty-four hour-a-day tracking was accomplished in two shifts, changing approximately at 0600 and 1800 Pacific Time

Acoustic tracking.—In 2002 and 2003, movements of acoustic-tagged cutthroat trout were monitored passively via stationary acoustic receivers. The locations of the receivers (Vemco VR2) are indicated on Figure 1 (for 2003). As with the radio telemetry receiver locations, deployment of the acoustic receiver array varied slightly between 2002 and 2003 though areas of coverage were consistent between years with 50-60 receivers deployed at any one time. Because these units were moored using a buoy and anchor system, positions changed within year as well as when units were retrieved and redeployed. Receivers were deployed near the surface as described in Clements et al. (2005). Notable differences between 2002 and 2003 were the deployment of three receivers near Sand and East Sand Islands to cover movements of fish from the Chinook River in 2002 (not shown in Figure 1) and the addition of three receivers deployed in the mouths of Germany, Abernathy, and Mill creeks in 2003. As with radio telemetry data (above), observations were considered to be duplicate if occurring at the same point within a 10 min interval. The time of duplicate observations were averaged for analysis.

There was no active tracking of acoustic tagged fish in 2002, but in 2003 efforts were made to track by boat using a directional towed receiver (Vemco VR 28). This effort was largely unsuccessful due to boat equipment failure, producing a single track. The tracking protocol was the same as that described for active radio tracking above.

Gill Na$^+$,K$^+$-ATPase activity determination.—Gill Na$^+$,K$^+$-ATPase activity was determined using the microplate method described by McCormick (1993) as validated for cutthroat trout (Zydlewski, unpublished). Briefly, gill tissue was removed and immersed in 100 µL of ice cold SEI buffer (150 mM sucrose, 10 mM EDTA, 50 mM imidazole; pH = 7.3) and stored at -80 ^{o}C. Gill samples were thawed immediately prior to assay and homogenized in 200 µL of 0.1 % sodium deoxycholate in SEI buffer. The homogenate was centrifuged to remove insoluble material. Specific activity of Na$^+$,K$^+$-ATPase was determined in duplicate by measuring ATPase activity with and without 0.5 M ouabain in a solution containing 4 U/mL lactate dehydrogenase, 5 U/mL pyruvate kinase, 2.8 mM phosphoenolpyruvate, 0.7 mM adenosine triphosphate (ATP), 0.22 mM nicotinamide adenine dinucleotide (reduced)(NADH), 50 mM imidizole, 45 mM NaCl, 2.5 mM MgCl$_2$, 10 mM KCl; pH = 7.5. Kinetic analysis of ATP hydrolysis was measured at 25 ^{o}C by monitoring [NADH] at 340 nm using a 96-well plate reader. Protein concentration of the gill homogenate was determined in triplicate using the bicinchoninic acid (BCA) method (Smith et al. 1985; BCA Protein kit, Pierce, Rockford, IL, USA) using bovine serum albumen as standard. Activity of gill Na$^+$,K$^+$-ATPase is expressed as µmol ADP • mg protein^{-1} • h^{-1}.

Statistics and calculations.—Significance of statistical analysis is reported at the p < 0.05 level. Two-way ANOVA was used to analyze length, weight, condition factor (Table 1), and gill Na$^+$,K$^+$-ATPase activity (Table 2) using year and tributary (Germany, Mill, and Abernathy creeks) as factors. Significance of factors or of interactions was followed by analysis within each factor. One-way ANOVAs were used for comparison within each year where significance was found. An inclusive one-way ANOVA was also run for all groups to include unbalanced groups. In all analyses, significance with a one-way ANOVA was followed by a Tukey's post-hoc test. Intervals about a mean are reported as ± one standard error (SE) or standard deviation (SD) as indicated.

Calculation of time to reach the Columbia River mouth (Table 2) was based on first observation of a tagged individual at or downstream of river kilometer 20 (this was the lowest point in the system where radio tags could be reliably detected due to salinity). Two speed calculations are shown using initial time from release after tagging and last observation of tagged individual at (or upstream) of rkm 85, respectively (to allow for variation in recovery from tagging and resumption of migration). Significance within these data using Kruskal-Wallis (using either tributary or year as factors) was followed by Mann-Whitney U tests for multiple comparisons. Individual values of gill Na$^+$,K$^+$-

TABLE 2.—Mean gill Na$^+$,K$^+$-ATPase $\pm$ 1 SE (expressed as µmol ADP • mg protein^{-1} • h^{-1}) and median speed of tagged cutthroat trout from of time of tagging and time of departure from tagging area, respectively, to first detection at rkm 20 or lower. There are no statistical differences between mean gill Na$^+$,K$^+$-ATPase activities. Significance between medians for 2002 and 2003 by Mann-Whitney *U* test is indicated by "*".

Year	Source	Gill Na$^+$, K$^+$-ATPase (:ADP • mg prot^{-1} • h^{-1})	Days to reach Columbia River mouth			
			From tagging		From departure	
			Medium	Range	Medium	Range
2002	GERM	3.4 ± 0.18 (17)	6.1	2.3 – 18.9 (8)	5.6	1.7 – 17.8 (8)
	ABER	3.7 ± 0.25 (32)	9.4	2.2 – 31.8 (20)	6.1	1.0 – 31.8 (20)
	MILL	3.5 ± 0.21 (52)	5.8	2.2 – 27.7 (23)	5.5	1.0 – 27.7 (23)
	CHIN	3.7 ± 0.38 (23)	na	na	na	na
	ALL	*3.6 ± 0.13 (124)*	*6.6*	*2.2 – 31.8 (51)*	*5.5*	*1.0 – 31.8 (51)*
2003	GERM	2.8 ± 0.24 (22)	6.2	1.1 – 37.1 (8)	2.4	1.0 – 33.9 (8)
	ABER	3.5 ± 0.53 (14)	4.5	2.0 – 7.0 (6)	3.9	2.0 – 6.7 (6)
	MILL	3.5 ± 0.30 (23)	3.5	2.3 – 25.0 (10)	3.2	2.0 – 25.0 (10)
	ALL	*3.2 ± 0.19 (59)*	*4.3*	*1.1 – 37.1 (24)*	*3.2*	*1.0 – 33.9 (24)*

ATPase were compared with individual speed to reach the river mouth using a linear regression.

To consider patterns of directed movement in the context of tidal and diel cycle, observations from active radio tracking in 2003 were analyzed. Of those individuals, only those that had tracks that lasted more than 48 h and met the criteria described below were considered. "Directed movement" is defined as a movement parallel to the Columbia River shipping channel (as demarked by the US Coast Guard buoy system), with downstream movements being defined as positive and upstream movements being defined as negative.

Speeds for these analyses were calculated from position data collected at intervals of less than one hour, but greater than 10 min. Exclusion of observations at intervals less that 10 min was necessary to prevent erroneously high speed calculations based on fluctuations in Global Positioning System (GPS) position measurements. Speeds greater than 11 km/h were rejected as this represented the greatest directly observed speed during tracking efforts. Time used in calculations described below was an average of the two observed positions.

Tidal reference was determined using tidal predictions of National Oceanic and Atmospheric Administration (NOAA) from Skamokawa, Washington (rkm 54, 46° 16 N 123° 27 W) which represented an approximate midpoint in the range of observations from rkm 20 to rkm 91. Tides can differ through this reach by approximately 2 h based on data from Astoria (-1 h, rkm 20; 46° 12 N 123° 46 W) and Stella, Washington (+1 h, rkm 91, 46° 11' N 123° 7' W). Data

were not interpolated for the fish location. Based on tidal predictions, a tidal cycle was defined as a continuum from 0 to 1, with 0 defined as high tide and 0.5 defined as low tide (regardless of whether the cycle represented a spring or neep tide).

Similarly, data for the diel cycle experienced by moving fish was based on prediction for Skamokawa, Washington. To consider diel cycles under a changing day length, the photoperiod was defined to a range of values between 0 and 1, with sunrise being 0 and 0.5 being defined as sunset. Because the photoperiod was changing (14.2 h light on May 1 to 15.4 h on June 30) when tracking occurred, the absolute time assigned to a value of "0" and "0.5" changed through the season but continued to represent sunrise and sunset.

For both tidal and diel representations, calculated directed speeds of a fish were assigned values in the tidal or diel cycle continuum. (For example a fish assigned 0.1 and 0.3 for diel and tidal cycles respectively would have been observed in the early morning on an outgoing tide). Individuals that did not have more than ten values in each of ten bins were excluded from analysis. For each individual and each bin the 25th, 50th, and 75th percentiles were calculated. Averages of these values for all fish are presented in Figure 2. Differences in averages of the 50th percentile were analyzed via one-way ANOVA (using tidal or diel bins as a grouping variable). Significance with one-way ANOVA analysis was followed by a Tukey's post-hoc test.
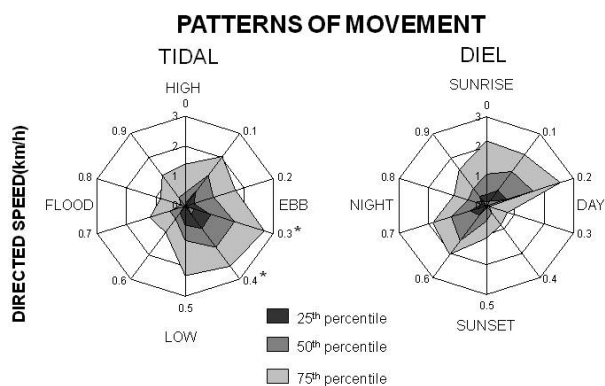
PATTERNS OF MOVEMENT

FIGURE 2.—Downstream movement patterns of coastal cutthroat trout implanted with radio tags in 2003 and actively tracked by boat. The radial graphs represent movements with relation to tidal cycle and diel cycle. For tidal cycle "0" is defined as high tide, 0.5 as low tide. For diel cycle "0" is defined as sunrise and "0.5" as sunset. Each polygon represents the average percentile (25th, 50th, and 75th) of 12 fish for which there was adequate data. (See materials and methods). Asterisks indicate significance between 50th percentile and lowest values.

Results

Downstream movement.—In 2002, 96 cutthroat trout were tagged with radio transmitters and released in Germany, Abernathy, and Mill creeks. From these fish, 91 tracks were collected and 5 fish were not observed after release. A total of 31,223 observations were made with 433 active and 30,790 passive observations. In 2003, 22 cutthroat trout were tagged with radio transmitters and released in Germany, Abernathy, and Mill creeks. From these fish, 17 tracks were collected and 5 fish were not observed after release. Some 9,072 observations were recorded—3,234 active and 5,838 passive.

In both years, the majority of fish displayed directed downstream movement (55/91 in 2002 and 17/22 in 2003; Figure 3). No fish was observed moving more that 3 km upstream after entry into the main stem of the Columbia River. Of those fish displaying downstream movement, the vast majority were subsequently observed at rkm 20 or lower in the system (49/55 in 2002 and 13/17 in 2003).

In 2002, 49 cutthroat trout were tagged with acoustic transmitters, 23 from Germany, Abernathy, and Mill creeks and 26 from the Chinook River. From these fish, 7,189 passive observations were collected and 32 tracks were collected. Seventeen fish were not observed after release. In 2003, 39 cutthroat trout were tagged with acoustic transmitters in Germany, Abernathy, and Mill creeks. From these fish, 13,022 observations were made, 280 during active tracking and 12,742 passive observations. Seven fish were not observed after release.
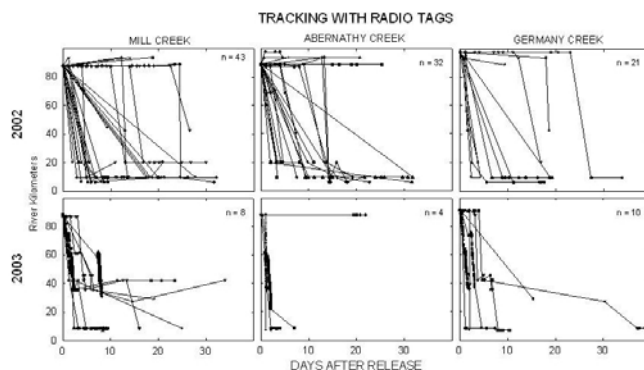

FIGURE 3.—Downstream movement data for coastal cutthroat trout implanted with radio tags in the mouths of up-river tributaries (Germany, Abernathy, and Mill creeks) of the Columbia River. The number of trout tagged for each tributary and year is indicated in the upper right corners of the graphs.

As with the radio telemetry, the acoustic tracks in 2002 and 2003 demonstrated rapid and directed downstream movement from Germany, Abernathy, and Mill creeks towards the mouth of the Columbia River (17/23 in 2002 and 12/39 in 2003; Figure 4). More than half of the fish observed to move downstream were observed at or in the ocean (rkm 0; 10/17 in 2002 and 7/12 in 2003). Similarly, in the Chinook River (2002) cutthroat trout rapidly moved downstream (14/26) and left the Columbia River (13/14; Figure 5).

For cutthroat trout leaving Germany, Abernathy, and Mill creeks in 2002, individuals took a median of 6.6 d to reach the mouth of the Columbia River from the time of tagging and a median of 5.5 d once movement had been initiated. In 2003, downstream movement was more rapid, moving to the mouth at median times of 4.3 and 3.2 d (p =
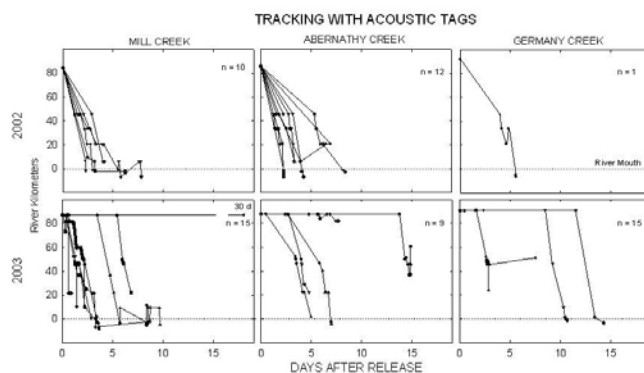

FIGURE 4.—Downstream movement data for coastal cutthroat trout implanted with acoustic tags in the mouths of upriver tributaries (Germany, Abernathy, and Mill creeks) of the Columbia River. The mouth of the Columbia River (rkm 0) is indicated with a dotted horizontal line. The number of trout tagged for each tributary and year is indicated in the upper right corners of the graphs.
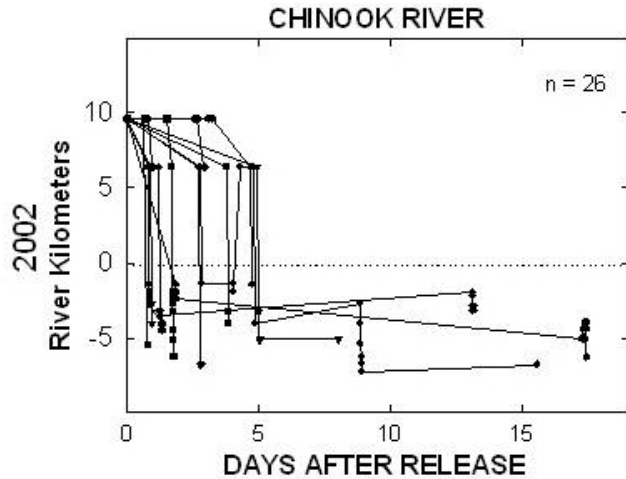
FIGURE 5.—Downstream movement data for coastal cutthroat trout implanted with acoustic tags in the mouth of the Chinook River. The mouth of the Columbia River (rkm 0) is indicated with a dotted horizontal line. The number of trout tagged for each tributary and year is indicated in the upper right corners of the graphs.

0.07 and p = 0.01, respectively). Several individuals did not initiate movement for as long as 23 d, followed by directed downstream movement.

Maps depicting the active tracks of four cutthroat trout are shown in Figure 6. Individual tracks lasted up to 6 d. Cutthroat trout were observed traveling at rates greater than 10 km/h. Conversely, tracks of fish were at times punctuated with long lulls in activity, often associated with changes in the tidal cycle. Cutthroat often traveled near shore; however several individuals were observed crossing the shipping channel, but also traveling in the channel for multiple hours.

Gill Na^+,K^+-ATPase activity from cutthroat trout did not differ between years or tributaries (Table 2). Average activities in 2002 and 2003 were 3.6 and 3.2 µmol ADP • mg protein^{-1} • h^{-1}, respectively. Gill Na^+,K^+-ATPase activity was positively correlated with the time it took successful individuals to reach the mouth of the Columbia River, but the relationship was extremely weak ($R^2 = 0.01$, p = 0.002, n = 64). When cutthroat trout that delayed the initiation of movement by 10 or more days are excluded, the relationship is marginally strengthened ($R^2 = 0.09$, p = 0.0005, n = 44).

Downstream movement patterns indicate an association of migration with tidal cycle and suggest an influence of diel cycle (Figure 2). These data represent the 12 fish that had sufficient observations to fit the criteria described above (see Materials and Methods) with a median of 137 observations (range 126–1561). Averages of these percentiles are represented in the figure. Tidal cycle influenced directed downstream speed (one-way ANOVA; p = 0.006); cutthroat trout exhibited greater rates of movement concurrent with the ebb tide and less directional movement during the flood tide. There was a marginally significant effect of diel cycle on downstream speed (one-
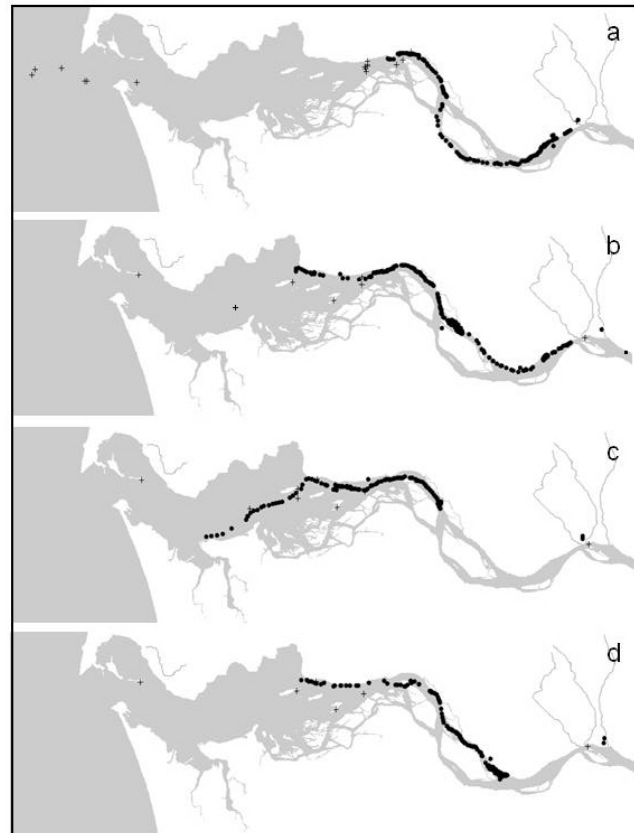

FIGURE 6.—Detailed tracks of cutthroat trout implanted with acoustic (a) and radio (b,c, d) tags in 2003. These representative tracks show both active and passive data ("•" and "+", respectively).

way ANOVA, p = 0.06), though no paired comparisons were significant. The data suggest greater movements just after sunrise and after sunset independent of tidal cycle.

Lengths, weights, and condition factors of tagged fish did not differ between tributaries or between years (Table 1). Average condition factor for all groups was 0.91 or less. The timing of tagging differed between years, May 5 to May 30 (mean of May 13) for 2002; May 9 to June 25 (mean of June 3) for 2003.

Discussion

Cutthroat trout tagged with both radio and acoustic tags in this study displayed directed downstream movement towards the ocean consistent with smolting behavior (Figures 3, 4, 5). Fish traveling from Mill, Abernathy, and Germany creeks to the mouth of the Columbia River exhibited travel speeds of 6.6 and 4.3 d from time of tagging and resumption of migration, respectively (Table 2). Many individuals traveled the distance in 1-2 d. Speeds were consistent with the movements of cutthroat trout tagged with passive integrated transponder (PIT) tags in these creeks and "recaptured" in the lower Columbia River (Zydlewski, unpublished data) using a PIT trawl (Ledgerwood et al. 2004). These speeds are also similar to

those observed in other anadromous salmonid smolts in the Columbia River and other rivers (Schreck et al. 2002).

The calculated speeds of movement from the time of departure of the tagging area to the mouth of the Columbia River differed between 2002 and 2003 (Table 2). In 2003, travel speed of migrants was nearly two-fold lower than that observed in 2002. A possible explanation for this difference is the timing of tagging differed between years. In 2002 migrants were tagged from May 5 to May 30 while in 2003 migrants were tagged from May 9 through to June 25. Based on flow data from the Columbia River (USGS data) fish in 2003 were tagged during a period of moderately higher flows than those in 2002. In addition to annual variations in river flow conditions, migrants experienced higher river temperatures in 2003, perhaps influencing migratory behaviors.

While most observations indicate a pattern of directed seaward migration, there are a number of fish for which there is either no data subsequent to tagging or only observations at or near the point of release. These fish could have lost their tag, not been detected by the receivers, not displayed migratory behavior, or been mortalities. Tagging is unlikely to be a direct cause of mortality. Immediate and delayed tagging mortality was rare (<1 %) in controlled tagging studies (Zydlewski, unpublished data). Likewise, tag loss is rare during the life of the tag. However, it can be assumed that surgical tagging is likely to affect short term performance (e.g. swimming speed; Adams, 1998) and may contribute to vulnerability to predation. While acoustic tags cannot be located out of water, six radio tags were recovered on the islands of the lower Columbia River (Rice and East Sand Islands; Figure 1), which harbor nesting colonies of Caspian terns *Sterna caspia* and double crested cormorants *Phalacrocorax auritus*. The birds inhabiting these colonies are known to impact salmonid smolt numbers in the Columbia River (Collis et al. 2001).

A minority of tagged fish may have not been migrating seaward when tagged; their capture could simply have been a result of local movements. For a small number of fish, the last observation was in the creek where they were tagged. In several cases, the fact that the fish was alive subsequent to remaining near the tag site was confirmed with electrofishing (one fish in 2003) and recapture of tagged fish in the rotary screw trap (four recaptures in 2002). In at least five cases, tagged fish entering the Columbia River traveled into the mouths of the neighboring creeks; two of the five were eventually observed at the mouth of the Columbia River. The possibility remains, however, that tagged fish were active migrants that ceased migratory behavior, possibly as a result of tagging.

Data from acoustic telemetry suggests that fish tagged in Mill, Abernathy, and Germany creeks and reaching the mouth of the Columbia River tended to exit the river mouth and move into the plume (Figure 4 and Figure 6a). At least three individuals were observed remaining in the area of the river mouth for 3-5 d before their last observation, apparently moving with the tide. This pattern appears to be consistent with the behaviors of juveniles exiting the Chinook River (rkm 6; Figure 5).

Once exiting the mouth of the Columbia River, the evidence suggests that the migrants leave the area of the river plume in the vicinity of the ocean array receivers. One tagged fish (from Abernathy Creek) was observed to have left the immediate area of the Columbia River mouth and traveled 65 km south in two weeks, near the Nehalem River mouth on the Oregon coast (where an unrelated acoustic tracking study was underway). This movement is consistent with observations that coastal cutthroat trout do not venture far offshore. Tipping (1981) surmised that coastal cutthroat trout from the Cowlitz River may not go far from the estuary of the Columbia River. Similarly the highest numbers of coastal cutthroat trout are caught from 10-45 km from the coast of Oregon and Washington (Johnston 1982). A relatively short sojourn to sea before retuning in the fall has been hypothesized to result in relatively high survival of returns (some 40% higher than other salmonids; Giger 1972).

The observed directed seaward movement described here differs from some observations where juvenile cutthroat trout evidently make greater use of the estuaries (Tomasson 1978; Trotter 1997; Lisa Krentz, Oregon Department of Fish and Wildlife, unpublished data). Variation in observed life history strategies among rivers should not be surprising. Migratory patterns for coastal cutthroat trout have been described as diverse, with both sea-run and river run (potamodromous) migratory behaviors being observed (Trotter 1997). However, the relative uniformity of seaward movements subsequent to entry into the main stem of the Columbia River (and the apparent absence of potamodromy) was unanticipated. It may be the case that rapid and directed downstream movement seaward may be the most advantageous migratory strategy in this and other large river systems. "Typical waters" supporting anadromous coastal cutthroat trout are generally small streams with low flow (Johnston 1982) possibly limiting competition from larger salmonids for spawning habitat (Pearcy 1990). Exploitation of the lower reaches of these small systems may therefore afford greater rearing opportunities.

The possibility that this somewhat uniform migratory pattern is a recent condition cannot be cast aside. Life history diversity of cutthroat trout may have declined in the Columbia River due to changes in the hydrograph. The impacts of hydropower on upriver salmonid stocks are understandably linked to passage (Deriso et al. 1996; Deriso 2001). In the lower Columbia River, however, regulated flow has resulted in a shift in the amplitude and timing of high flow events (PNRC 1978). This shift in hydrological character influences main stem flows, plume structure, salinity profiles, tidal range, and productivity (Bottom 2001). The shift in invertebrate community has likely altered the growth opportunities of juvenile salmonids that linger in the estuary (including cutthroat trout). It should be noted that this pattern of limited main stem Columbia River usage may be specific to the juvenile life history stage. Returning anadromous adults to the system have been

observed to use the main stem river more extensively (Mike Hudson, U.S. Fish and Wildlife Service, unpublished data).

Migrating juvenile cutthroat trout tracked by boat in this study often traveled near shore; however several juveniles were observed not only crossing the shipping channel (e.g., Figure 6a and 6c) but also traveling in the channel for several hours. This observation was unanticipated as an avoidance of open waters has been suggested (Jones 1976). Entry into the channel was often associated with the presence of formations (natural or human) that intersected with the flow of the water (e.g., pile dikes).

Downstream movements of coastal cutthroat trout were greatest on an outgoing tide (Figure 2). Patterns of tidal transport have been reported for many species (deVeen 1978; Locke 1997) including juveniles of spring Chinook, fall Chinook and steelhead trout in the Columbia River and estuary (Moore et al. 1998; Shreck et al. 2005). Trout using tidal currents to aid migration gain obvious energetic and navigation advantages. Observations in this study also suggest that downstream movement is greatest in the hours just after sunrise and just after sunset. While this data is limited, it is not unreasonable to hypothesize that downstream migratory behavior of cutthroat trout would be influenced by diel cycle as has been observed in other salmonids (Carlsen et al. 2004; Emmett 2004)

Smolting salmonids develop seawater tolerance coincident with migration as part of a complex developmental shift, the parr-smolt transformation. There is some correlation between gill Na^+,K^+-ATPase activity and the parr-smolt transformation in salmonids (Hoar 1976; McCormick and Saunders 1987; Hoar 1988), however we have insufficient data to do more than speculate as to the developmental state of the fish studied. Average gill Na^+,K^+-ATPase activity values (3.6 and 3.2 µmol ADP • mg protein^{-1} • h^{-1} for 2002 and 2003 respectively) are nearly two-fold higher than activities measured in coastal cutthroat trout captured in November 2002 (Zydlewski, unpublished data) but are lower than those measures in many smolt species (McCormick and Saunders 1987). It is reasonable to conclude from similar enzyme activities among streams and time that those fish tagged were of roughly similar developmental stage. While gill Na^+,K^+-ATPase activity should be viewed as an indirect indicator of smolting, it should not be viewed as a surrogate for more detailed physiological work including seawater challenges. There is some suggestion that gill Na^+,K^+-ATPase activity is related to downstream migration speed. As both metrics (behavior and Na^+,K^+-ATPase activity) are extremely variable, the relationship is understandably weak.

Based on these data, juvenile coastal cutthroat trout studied in these four tributaries to the Columbia River exhibited behavioral patterns that are consistent with those observed in other salmonid species. Juveniles leaving tributaries of the main stem Columbia River move in a rapid and directed fashion seaward. There was no indication that these fish displayed a potamodromous life history or lingered in the estuary (as is observed in some other systems). Because of these similarities, anthropogenic activities and management actions in the main stem Columbia River that influence salmon smolts are likely to affect anadromous coastal cutthroat trout smolts in a parallel fashion. It is important to note, however, that other life history stages may use the main stem and estuary habitat of the Columbia River more extensively.

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