Vertical and horizontal movements of adult chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary

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Maturing salmon leave oceanic feeding grounds and migrate towards their natal rivers, converging on coastal and estuarine waters. Although the passage through an estuary represents a physical and physiological milestone during the homing migration of salmon and is often a period of heavy commercial and sport harvest, relatively little is known about how oceanographic processes might affect the distribution of salmon. Estuaries are transition zones between coastal and riverine waters, and are areas of rapidly changing temperature, salinity, and current regimes which may present migrating fish with osmo- and thermoregulatory challenges. Furthermore, estuaries may also represent a transition zone for the orientation mechanisms salmon use to find their natal stream (McKeown 1984).

Several investigators have observed the horizontal movements of Atlantic salmon *Salmo salar* (Stasko 1975), sockeye salmon *Oncorhynchus nerka* (Groot et al. 1975), and chinook salmon *O. tshawytscha* (Fujioka 1970) in estuaries, and observed both passive and active movements with and into tidal currents. More recent tracking studies of maturing Atlantic salmon, sockeye salmon, chum salmon *O. keta*, and steelhead trout *O. mykiss* in coastal waters have demonstrated that their vertical movements may be related to the local vertical stratification of the water column (Westerberg 1982, Soeda et al. 1987, Quinn et al. 1989, Ruggerone et al. 1990). No studies are presently available which describe both the vertical and horizontal movements of salmon within an estuary.

The following study was designed to describe the short-term movements of adult chinook salmon in the Columbia River estuary outfitted with pressure-sensitive ultrasonic tags to (1) relate these movements to tidal currents and the temperature and salinity structure of the water column, and (2) examine how these movements might be explained by their physiology and the need for orientating clues.

Materials and methods

Study site description

The Columbia River has a large estuary with tidal influence extending approximately 161 km upriver from the mouth, although salt intrusion extends no more than 48 km upriver along the bottom (Simenstad et al. 1984). Average monthly river flows from 1969 to 1982 were 7460 m^3/s with a range of 4070 m^3/s in September to 10,530 m^3/s in June (Simenstad et al. 1984). This estuary has mixed semidiurnal tides; that is, each tidal day has two high and two low tides of unequal size (Jay 1984). The mean tidal range (mean high water to mean low water) measured over 138 tides in 1958 was 2.31 m at North Jetty (Fig. 1; Jay 1984).

Ultrasonic telemetry

Chinook salmon were captured during the morning of each tracking day with short (~5 min) drifts using 90–180 m of 21 cm stretched-mesh commercial gillnet (~12 m in depth) which fished the entire water column. When a fish was detected, the net was immediately retrieved, and the fish removed and placed in a 100 L cooler filled with surface water. If more than one chinook was captured, one was selected for tracking based on scale retention, lack of scars, and general activity level. Total length was measured to the nearest cm, and a numbered disc tag was attached below the dorsal fin. A pressure-sensitive (74 mm long × 16 mm in diameter) ultrasonic transmitter (Vemco Ltd.), weighing 13 g in water and calibrated within ±1 m to a conductivity/temperature/depth probe (CTD; InterOcean model 513) prior to the track, was inserted into the stomach of the unanesthetized fish. The fish was placed in the boat's partially-filled watertight fish locker (2.5×1.5×0.5 m) for recovery (~30–45 min). The holding tank allowed the fish to reach the surface, gulp air, and inflate its swimbladder. All fish were captured in

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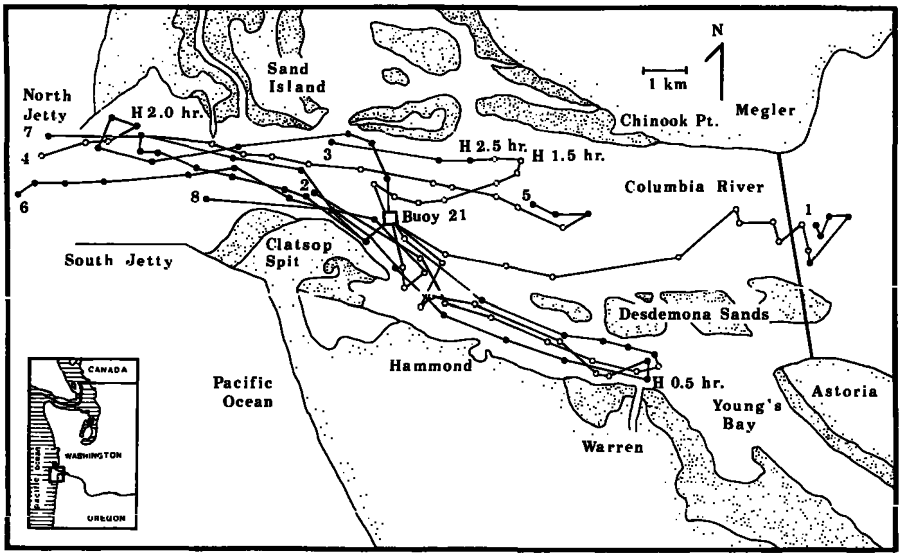

Figure 1
Study area and track maps of horizontal movements by chinook salmon *Oncorhynchus tshawytscha* tracked in the Columbia River estuary. Sampling during flooding (○) and ebbing (●) tides. Each circle represents 30 min of tracking time. 'H' indicates extended holding period occurred.

relatively shallow water (about 5 m) on the south side of Sand Island (except Fish 1 which was captured on the north side of Desdemona Sands), and all fish were released at Buoy 21 (Fig. 1).

A single fish was released each day and followed primarily during daylight hours from the gillnet vessel *Midnight Gambler*. Transmitted signals were received by a directional hydrophone and tunable receiver/decoder (Vemco Ltd.). During tracking, the boat typically stayed 50–400 m away from the fish, and the following data were collected: (1) boat position every 5 min from a loran C receiver; (2) water depth beneath the boat every 5 min from a fathometer; (3) fish depth every 1 min from the decoder; (4) approximately every 30 min the fish was more closely approached (usually to within 50 m, based on triangulation and signal strength), and secchi disk and CTD casts were made while the boat drifted. CTD casts took about 5 min to perform and measured the conductivity and temperature at intervals of 1 or 2 m, usually to within 4 m of the bottom. In deeper waters, casts were generally limited to 12 m to avoid losing the fish. Except for fish swimming close to the bottom, this range always encompassed the depth at which the fish was swimming and any large changes in temperature or salinity.

Data analysis

Boat positions were used to reconstruct each fish's path on a horizontal track map and to determine ground speed. A 15 min sampling interval was chosen to calculate ground speeds because shorter intervals may overestimate fish speed due to extraneous boat movements, and longer intervals may underestimate fish speed because calculations based on a straight line between positions may mask shorter-scale movements. Water and fish depths were used to reconstruct each fish's path on a vertical track map. Conductivity was converted to salinity (Perkin & Walker 1972) for construction of temperature and salinity profiles.

To determine whether salmon showed preferences for ranges of temperature or salinity, the salinity and temperature of the water experienced by each fish were determined indirectly by substituting the appropriate values from the temperature and salinity profile for the depth at which the fish was swimming during each observation. Salinities and temperatures between the measured depth-intervals were determined by linear interpolation. The range of temperatures and salinities available to each fish was determined from temperature and salinity profiles separated into 1-unit (°C or ‰) intervals. The fraction of the water column that each unit of temperature or salinity occupied within the sampled depth was calculated and multiplied by the time-interval of the representative temperature and salinity profile. Each temperature and salinity profile was assumed to represent water conditions over a time-interval midway between consecutive profiles. Fish that swam near the bottom sometimes exceeded the depth of the CTD casts, and these observations were omitted from analysis of salinity or temperature preference. Frequencies of temperature and salinity were summed over all profiles for each track to obtain the salinity and temperature distribution available to each fish. These distributions were tested statistically by goodness-of-fit analysis to determine if the distributions of available and experienced conditions were similar. Differences were assumed to indicate fish were displaying non-random vertical movements, presumably to select for a favorable combination of environmental factors.

Results

Eight chinook salmon were tracked in the Columbia River estuary from 27 August to 5 September 1987, resulting in 56:39 h of tracking time over more than 127 km (Table 1). Mean river flow over Bonneville Dam during the study period was 2910 m^3/s (range 2370–3430 m^3/s; Fish Passage Center, Corvallis OR). Secchi disc measurements taken intermittently during all tracks had a pooled average depth of 2.47 m (range 1.43–4.12 m for individual tracks). In general, signal reception in the estuary was good and no fish were lost during the tracking period. Tracking of a fish was terminated owing to danger of vessel stranding on mudflats (Fish 1), high waves at the river entrance sandbar (Fish 2,4,8), darkness (Fish 3), or fish movement into the ocean (Fish 6,7). Only Fish 5 was followed during periods of darkness (1:09 h). Five of the eight fish (Fish 2,5,6,7,8) had dark or dusky skin color, indicative of lower-river stocks known as tules. Bright-skinned fish (Fish 1,3,4) may have derived from either tules or upriver brights. All upriver brights enter the river with a more "oceanic" appearance and return to spawning grounds and hatcheries primarily near the Hanford Reach (Howell et al. 1984); however, some tules also enter the river in bright ocean-type condition.

Horizontal movements

Fish usually moved in the direction of the prevailing tidal current, and reversals in direction and a milling/holding behavior were often associated with changing tides (Fig. 1). The average ground speed (weighted by the number of sampling intervals) for tracked fish was 2.33 km/h (range 1.28–3.17 km/h for individual fish (Table 1). Ground speeds are the resultant of two vectors: velocities (speed and direction) of the tidal current and of the tracked fish. When analyzed by tidal stage, mean ground speeds for individual fish ranged from 0.74 to 4.08 km/h (2.60 overall) during ebbing tides, and 0.91 to 3.12 (2.04 overall) during flood tides (Table 2).

Two chinook salmon were recovered after the tracking period. Fish 2 was recaptured 14 d after release during test fishing operations 93 km from the river mouth, and Fish 7 was recaptured 9 d after release by a sportsman about 80 km from the river mouth. These fish had net travel rates of 6.0 and 7.8 km/d, respectively, after release.

Vertical movements

Mean fish depth was 5.5 m, and mean water depth beneath the boat was 13.4 m (Table 3). Vertical profiles of temperature and salinity indicated extremely dynamic hydrographic regimes. Within a single track, some profiles indicated nearly uniform temperatures and salinities over all depths, while others revealed strong haloclines and thermoclines. Vertical track maps (Fig. 2), and fish-depth frequency distributions relative to mean temperature and salinity profiles (Fig. 3) for Fish 4 and 5, show two observed patterns of vertical movement: Some salmon swam in brackish surface waters with large vertical gradients of salinity and temperature and made occasional excursions into uniform bottom waters (Fish 2,6,7,8), whereas others demonstrated periods of swimming in the water column and near the bottom (Fish 1,3,4,5). Some vertical track maps show fish that appear to be deeper than

Table 1

Summary statistics for tracks of adult chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. Gross distances traveled and average speeds were based on 15 min sampling periods.

Fish	Release date	Release time	Fish total length (cm)	Time tracked (h:min)	Gross distance traveled (km)	Mean ground speed (km/h)	Reason for ending track
1	Aug. 27	11:12	91	7:18	11.73	1.89	Possible vessel stranding
2	Aug. 28	12:53	84	6:29	18.52	2.96	High waves at river entrance
3	Aug. 29	12:19	86	7:44	9.75	1.28	Darkness
4	Sept. 1	10:55	76	7:20	16.16	2.23	High waves at river entrance
5	Sept. 2	10:12	96	10:52	24.41	2.26	Darkness
6	Sept. 3	10:44	83	4:26	12.29	2.89	Movement into ocean
7	Sept. 4	09:57	76	4:33	14.27	3.17	Movement into ocean
8	Sept. 5	09:40	81	7:57	20.56	2.65	High waves at river entrance
Mean			84	7:05	15.96	2.33	
Total				56:39	127.69		

Table 2

Mean ground speeds and sample sizes during ebb and flood tides based on 15 min sampling intervals for chinook salmon *Oncorhynchus tshawytscha* tracked in the Columbia River estuary.

	Ebb		Flood	
Fish	Ground speed	Sample size	Ground speed	Sample size
1	0.74	15	3.12	14
2	4.08	9	2.34	16
3	1.86	12	0.19	19
4	2.98	17	1.17	12
5	1.71	5	2.54	21
5	2.09	17		
6	3.01	15	2.01	2
7	4.09	11	1.73	7
8	3.10	15	2.24	16
Pooled	2.60	116	2.04	107

the bottom. This resulted from recording water depth under the boat, which generally followed a short distance behind the fish rather than directly above it. Although this discrepancy makes it impossible to accurately determine the distance of the fish from the bottom, Fish 1 and Fish 3 spent the majority of their time close to or on the bottom, and Fish 4 spent approximately 35% of its time near the bottom.

Fish encountered a wide range of salinities (7.8–33.6‰) and temperatures (8.9–22.9°C; Table 3). Due to the dynamics of tidal currents and vertical water structure within the estuary, the frequency distributions of available salinities and temperatures were different for all fish tracks (log-likelihood test, Zar 1984; $p<0.001$). Hence, it was impossible to compare the distributions of temperature and salinity experienced by individual fish. No analysis was made on the depth data transformed to salinity and temperature for portions of fish tracks below depths sampled by the CTD, because the available frequency distributions of salinity and temperature could not be calculated for these depths and the distance from the fish to the bottom could not be accurately determined. Due to these problems, an average of 83.2% (range 50.9–100%) of the depth observations for individual tracks were converted to experienced salinity and temperature. Fish 3 was not analyzed for temperature and salinity preference because it spent nearly all its time below depths sampled with the CTD. However, the frequency distributions of temperatures and salinities occupied by fish showed modes between 14° and 16°C for five of seven fish, and 17 and 19‰ for four of seven fish (e.g., Fish 4 and 5, Fig. 4). The log-likelihood test indicated that all fish occupied different distributions of temperature and salinity than they would have experienced by random vertical movements in their environments ($p<0.001$).

Discussion

In general, the tracked fish moved with tidal currents, milled during periods of low current velocity, and reversed their direction of movement with the change of tides. The results suggest that tidal currents are a major component to horizontal fish movements in the Columbia River estuary. Chinook salmon had higher mean ground speeds during ebbing tides than during flooding tides, presumably because tidal and riverine flows are additive during ebbing tides and antagonistic during flooding tides.

These findings tend to agree with other estuarine tracking studies (Groot et al. 1975, Fujioka 1970) of Pacific salmon. Fujioka (1970) found that the position of chinook salmon tracked in the Duwamish River estuary was dependent on the tidal stage, with fish generally

Table 3

Mean, maximum, and sample size of fish-depth observations; mean, minimum, and maximum water depth beneath the tracking boat; and fish-depth observations transformed to salinity and temperature experienced by tracked chinook salmon *Oncorhynchus tshawytscha* within the Columbia River estuary. CTD = conductivity/temperature/depth probe.

	Fish depth (m)			Water depth (m)				Salinity (‰)			Temperature (°C)			
Fish	Mean (SD)	Max.	*N*	Mean (SD)	Min.	Max.	*N*	Mean (SD)	Min.	Max.	Mean (SD)	Min.	Max.	Max. CTD depth (m)
1	4.6 (1.9)	10.2	406	5.8 (2.7)	1.2	12.5	89	12.9 (3.6)	7.8	19.8	17.0 (2.0)	13.0	22.9	12
2	2.0 (1.0)	8.1	374	12.1 (2.9)	6.7	18.3	78	16.0 (3.4)	8.0	27.4	16.8 (1.9)	11.8	20.0	12
3	17.1 (5.7)	24.9	440	16.5 (3.6)	7.9	23.8	92							10
4	7.9 (5.6)	22.3	405	14.6 (4.9)	3.7	29.3	89	18.4 (5.5)	9.1	32.7	15.0 (2.1)	8.9	18.1	12
5	2.1 (1.6)	24.2	618	14.2 (7.3)	4.3	30.5	129	20.4 (3.8)	13.0	32.6	14.4 (1.3)	9.4	16.8	14
6	2.3 (1.7)	9.5	249	16.2 (5.6)	7.9	29.3	51	25.5 (3.4)	16.8	32.3	13.6 (1.5)	10.5	16.0	12
7	3.3 (3.6)	16.1	235	15.4 (6.4)	7.0	30.2	55	25.3 (5.2)	17.4	33.6	13.0 (1.8)	8.9	15.5	10
8	2.8 (1.2)	10.8	437	13.7 (2.9)	6.7	19.8	92	18.7 (2.3)	10.6	31.3	15.6 (1.1)	10.0	19.1	12
Pooled	5.5 (3.3)	24.9	2675	13.4 (4.9)	1.2	30.5	675	19.4 (3.8)	7.8	33.6	15.1 (1.6)	8.9	22.9	

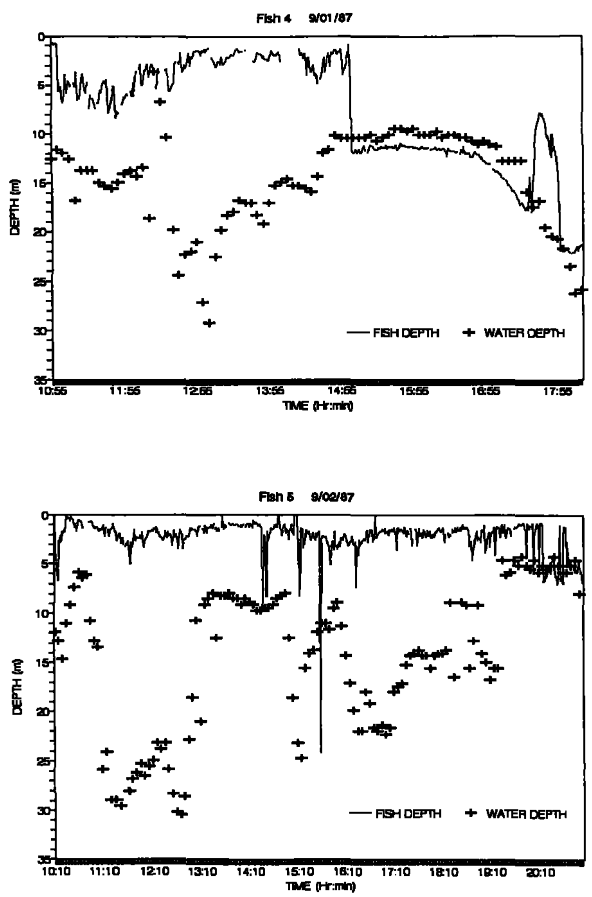

Figure 2

Track maps of vertical movements by Fish 4 and 5 within the Columbia River estuary.

further upstream during a high tide compared with a preceding or subsequent low tide. Similarly, Groot et al. (1975) found that sockeye salmon tracked in the Skeena River estuary tended to drift with the current. They also observed that during ebb tides, some fish exited the estuary and relatively few fish made any net movement upriver. Average ground speeds were slightly higher for Columbia River chinook (2.41 km/h) than the Skeena River sockeye (1.81 km/h in 1969 and 2.25 km/h in 1970), but these differences may merely reflect the tidal current regimes of the two estuaries.

Previous tagging studies have demonstrated that delays in estuaries of about one month are common in Pacific salmon (Wendler 1959, Verhoeven & Davidoff 1962, Vernon et al. 1964). Based on the period when marked fall chinook salmon are captured in the Columbia River commercial gillnet fishery, lower river tules delay in the estuary but upriver brights pass through relatively rapidly (Donald O. McIssac, Oreg. Dep. Fish Wildl., Portland, pers commun.). The movement of tracked fish with tidal currents and the lack of substantial net upriver progress support the hypothesis that fall chinook may spend an indeterminate amount of time holding within the estuary prior to upstream movements.

Tracked chinook displayed two vertical movement patterns: swimming close to the bottom, or a combination of swimming in midwater and close to the bottom. Time spent near the bottom may have been an alternative stock-specific behavioral pattern for tracked fish, or may have been influenced by stress from the capture and tagging procedure. Sockeye salmon tracked in deeper waters and for longer periods than the present study demonstrated characteristic vertical and horizontal movements about 1 h after release (Quinn et al. 1989). Stressed fish would be expected to show lethargic vertical and horizontal movements, and, as such, fish in the present study were considered to be behaving normally because all fish demonstrated substantial vertical movements during portions of their tracks.

The vertical distribution of salmon in estuaries may be in-

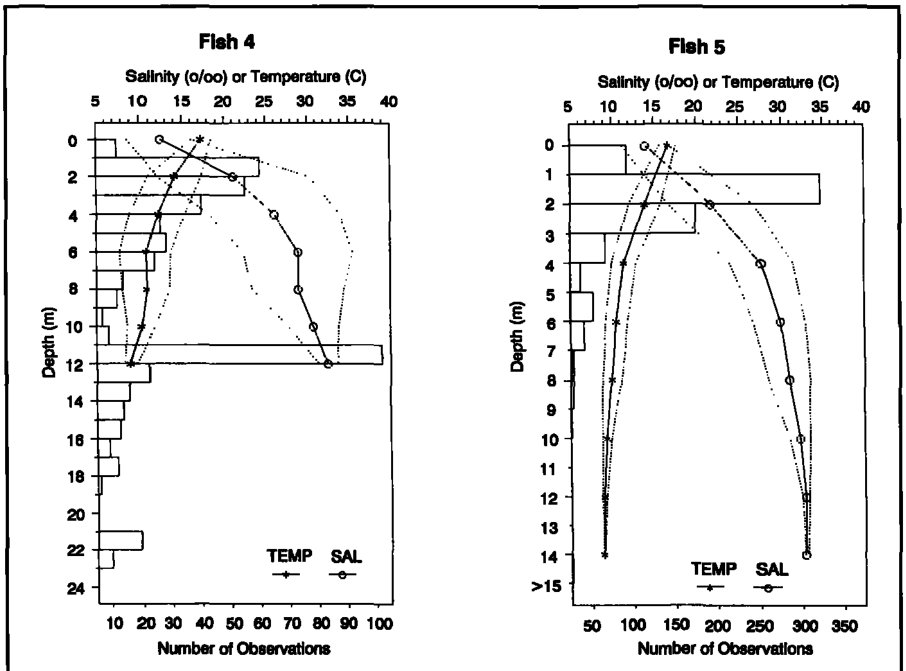

Figure 3

Mean temperature and salinity depth profiles and depth distributions for tracks of Fish 4 and 5. Dotted lines indicate 1SD.

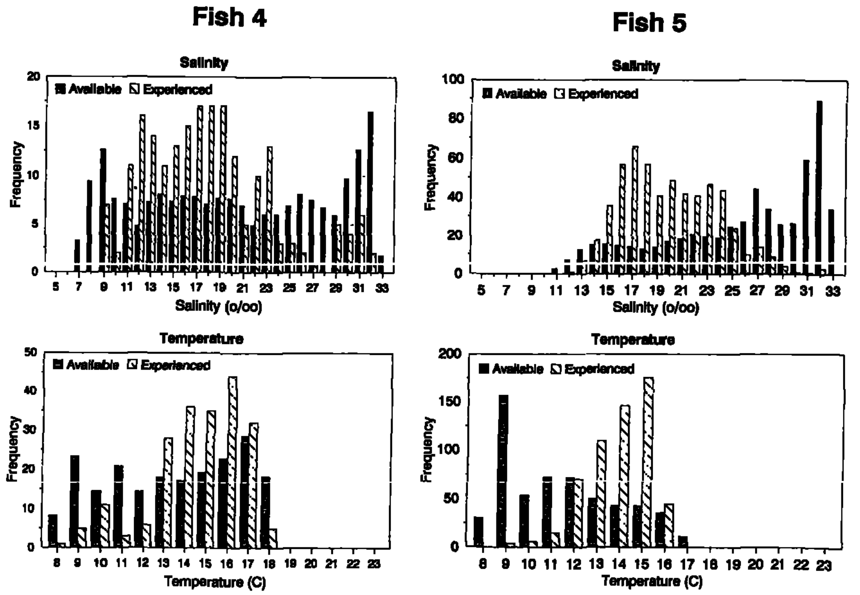

Figure 4
Histograms of experienced and available temperature and salinity distributions for Fish 4 and 5.

the present study were not minimizing their energy-expenditure rate while swimming in midwater, as they did not prefer the coolest water. Indeed, several often occupied relatively warm water (Fig. 5, Table 3). In contrast to the dark- and dusky-skinned fish which swam primarily in midwater, the three bright fish (Fish 1,3,4) potentially from upriver stocks swam for substantial periods near the bottom and may have been attempting to minimize their energy expenditures by utilizing the coolest waters available to them in the water column.

In contrast, a fish's preferred mean external salinity may be affected by its current physiological status and the degree to which the osmoregulatory system has switched its direction of active ion transport. Vertical salinity and temperature gradients are often correlated in estuarine environments, and the maturity level of a tracked fish is unknown; therefore, determining the degree to which salinity or temperature affect vertical movements is confounded in field experiments.

Fish orienting to olfactory stimuli (Hasler & Scholz 1983) might be expected to move up and down through the halocline (Westerberg 1982, 1984), and fish tracked in the Columbia River estuary were observed at depths containing large vertical gradients of salinity and temperature. Olfaction is an important component in homing by salmonids in rivers and streams (Hasler & Scholz 1983), but it is unclear to what extent and how olfaction is utilized for orientation in coastal and estuarine waters. Westerberg (1984) hypothesized that salmonids might derive information from the current shear at haloclines separating water layers containing different concentrations of natal river olfactants. Tracking data on Atlantic salmon *Salmo salar* by Westerberg (1982) and Doving et al. (1985) supported this hypothesis, demonstrating characteristic and regular dives to the halocline one or two times per hour. Data for Pacific salmon and steelhead trout in coastal waters (Ichihara & Nakamura 1982, Quinn & terHart 1987, Soeda et al. 1987, Quinn et al. 1989, Ruggerone et al. 1990) show a less clear pattern of vertical movements relative to the thermocline than that reported by Westerberg (1982) and Doving et al. (1985). Results of sockeye tracking (Quinn & terHart 1987, Quinn et al. 1989) in both mixed and stratified waters demonstrated

fluenced by species- or stock-specific preferences for particular temperature or salinity regimes, light levels, positions in the water column (relative to the surface or bottom), or by the need to locate orientating clues. Our observations of tracked chinook making vertical movements through large ranges of salinity and temperature indicate that they are tolerant of rapid, short-term changes in these features over several minutes, but utilized intermediate salinities and intermediate-to-warm temperatures while swimming in midwater. The presence of a lag time in equilibrating internal and external ion concentrations and temperatures could explain their ability to tolerate rapid changes in these factors because adult chinook salmon have been observed to require 30–60 min to equilibrate their internal temperature to ambient water temperature when moved between 19° and 9°C, depending on direction of the transfer and size of the fish (Berman & Quinn 1991).

Vertical movements which determine long-term internal temperature may be affected by energetic factors related to stock origin. Stocks such as upriver brights which have extensive in-river homing migrations might be expected to take advantage of the cooler water near the bottom of the estuary. Brett & Glass (1973) reported that oxygen consumption for a 5 kg sockeye salmon would be about 20–40% less in 10° than 20°C water, depending on whether the fish was at rest or active. Assuming a similar relationship for chinook salmon, most fish characterized as tules in that fish were generally surface-oriented in mixed waters and remained at or below the thermocline in stratified waters. In contrast, steelhead trout spent up to 96% of their tracked time within 1m of the surface, but made occasional dives through the thermocline/halocline located 5–7 m below the surface (Ruggerone et al. 1990). Ichihara & Nakamura (1982) reported that chum salmon *O. keta* in coastal waters off Japan spent 44% of their time within 5 m of the surface, and seldom dove through the thermocline. On the other hand, Soeda et al. (1987) reported that a chum salmon tracked for 57 h off the north Hokkaido coast spent much of its time swimming within the thermocline.

The vertical salinity and temperature profiles in this study showed that water structure ranged from uniform to highly stratified during a single tracking period. Chinook spent most of the tracked time either close to the bottom or within the salinity gradient, i.e., within the water layers predicted by Westerberg's (1984) hypothesis. Tracking studies of Atlantic and Pacific salmon suggest that the vertical movements of salmonids may be influenced by haloclines or thermoclines, but do not always demonstrate a consistent pattern of vertical movements relative to the water structure. These differences suggest that salmonids may have multiple mechanisms for orienting during their homing migrations which may change according to level of maturity, proximity to the home river, and the vertical water structure.

Moreover, if salmon derive directional information from current shears at the halocline, they may be able to maintain directed swimming using other guidance mechanisms (e.g., sun or magnetic compass). If so, only occasional excursions through the halocline may be sufficient for orientation, and other factors may affect their position in the water column. Thus, variation in vertical movement patterns among species and study sites does not contradict Westerberg's (1984) hypothesis.

In summary, tracked chinook salmon demonstrated no substantial net upstream movements while under observation, and tidal currents were a major factor influencing their horizontal movements. Two patterns of vertical movements were observed: Fish tended to swim in surface waters where salinity and temperature gradients were greatest, or they swam near the bottom. Vertical movements may have been influenced by temperature and salinity preferences related to stock origin and individual physiological requirements, or movements may have been used as a searching strategy for clues to orientation. Despite the lack of net upstream horizontal movements, the vertical movements of tracked chinook tended to support predictions that the vertical distribution of homing salmonids are influenced by water column structure which may be utilized for orientation towards natal river systems (Westerberg 1984).

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