

Observations on the Effect of Visual and Olfactory Ablation on the Swimming Behavior of Migrating Adult Chum Salmon, *Oncorhynchus keta*

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Abstract The behavior of chum salmon, *Oncorhynchus keta*, was studied using ultrasonic telemetry in the waters off the Okhotsk coast of Hokkaido from 1979 to 1981. Thirty-six adult fish were outfitted with a 50 KHz ultrasonic transmitter provided with either a depth sensor, depth/illumination sensors, or depth/temperature sensors. Twenty-one of the experimental fish were used as controls and left intact. Of the remaining fish, six had their sight destroyed, seven had their olfactory nerves severed or their nares filled with wax, one had both senses destroyed, and one had a sham operation, but had only a shallow transverse cut made in the skin over the olfactory nerves. Control fish and the fish with the sham operation initially swam in a horizontal zigzag pattern while fish with an obliterated sense swam in a similar pattern but to a reduced extent. The horizontal and vertical speeds of the intact fish were faster than those of the fish with a destroyed sense. Amplitude of vertical movements of the intact fish stretched from surface to bottom, while fish with destroyed vision tended towards midwater. Fish without an olfactory sense tended to be at the surface or near the bottom. Regular vertical movement would be effective in refreshing olfactory epithelia which might become acclimated when exposed to one odor. The vertical movements can be found in the horizontal zigzag movements in coastal and near shore migrations, as well as in the stream phase of homing. The zigzag movements, both horizontal and vertical, allow the fish to sense the water masses and locate the correct tributary.

The migration of salmon from oceanic feeding grounds to their home stream spawning site involves orientation and homing ability in the open ocean, coastal waters, and streams (Neave, 1964; Quinn and Groot, 1984). An olfactory basis for this homing ability for the final stages of riverine migration was presented by Hasler and Wisby in 1951, proposing that juvenile salmon become imprinted with the distinctive chemical odor of their natal stream and adult fish utilize long-term olfactory memory to locate their home stream during the spawning migration. In 1954, Wisby and Hasler conducted the first systematic field experiment confirming this olfactory hypothesis in coho salmon, *Oncorhynchus kisutch*, later demonstrated the hypothesis by Quinn et al. in 1989. Subsequent studies have shown similar findings for brown trout, *Salmo trutta* (Shearer, 1959), landlocked sockeye salmon, *O. nerka* (Lorz and Northcote, 1965), chum salmon, *O. keta* (Hiyama et al., 1966), chinook salmon, *O. tshawytscha* (Groves et al., 1968; DeLacy et al., 1969), and cutthroat trout, *O. clarki* (= *S. clarki*) (Jahn, 1969).

During the freshwater homing phase, coho salmon

are attracted by chemical cues (Scholz et al., 1972, 1975, 1976), which are used during upstream migration (Johnsen and Hasler, 1980). Hasler and Wisby (1951) proposed that rocks, soil and plants create a unique bouquet in each river and that salmon recognize their home river on the basis of these odors. In contrast to this hypothesis, Nordeng (1971, 1977) and Solomon (1973) postulated that adult salmonids are attracted to population-specific odors, pheromones, from juveniles residing in freshwater and migrating to sea. Adult salmonids are attracted to the chemical traces of conspecific juveniles (Selset and Doving, 1980; Quinn et al., 1983; Foster, 1985) and adults (Newcombe and Hartman, 1973; Emanuel and Dodson, 1979; Honda, 1980, 1982; Groot et al., 1986).

Detection of differences in the chemical makeup of waters within the stream is accomplished by zigzag swimming patterns (Johnsen and Hasler, 1980; Johnsen, 1981). In the coastal waters movement of Atlantic salmon, *Salmo salar*, when monitored with ultrasonic telemetry, has been related to finescale vertical layering of the water (Westerberg, 1982;

Døving et al., 1985).

In spite of considerable research effort, many aspects of homing are still poorly understood (Quinn, 1990). This study presents data from ultrasonic tracking of the swimming behavior of migrating adult chum salmon in the coastal waters off Japan. The effect of removal of olfactory and/or visual senses on migratory behavior is also presented and discussed. The present paper deals with two important behavioral aspects displayed by homing adult chum salmon, orientation to home stream ranges and locomotor patterns in the coastal waters.

Materials and methods

A total of thirty-six adult chum salmon (*Oncorhynchus keta*) was used in the present telemetric study during the fall spawning migration over three years (1979–1981). Thirty of the fish were captured 1.5 km upstream from the mouth of the Abashiri River at a fish hatchery trap (riverine origins of the fish were the Abashiri River) and six were taken at set net sites established along the coast adjacent to the mouth of the river (riverine origins of the fish were unknown). Fish were transported on a research vessel to the release site at sea. Data on fish sizes, capture sites (riverine origins of the fish), treatment, and tracking are presented in Table 1.

Twenty-one fish were left intact as controls. Vision was ablated in six fish by injection of 0.3–0.4 ml of 3% benzethonium chloride solution into the vitreous humor. Olfactory ablation was done by cutting the olfactory nerves midway between the nares and eyes in three fish, or by injection of wax (composed of citrus fruit and carnauba waxes) into the nares in four fish. In one fish both vision and olfaction were ablated by ocular injection and severing of the olfactory nerves. One fish received a sham operation which consisted of making a shallow transverse cut in the skin over the olfactory nerve tract. Ultrasonic transmitters were inserted into the stomach via the esophagus (one-channel transmitter) or affixed to the base of the anal fin (two-channel transmitters). Fish were anesthetized with 0.1% tricaine methane sulfonate (MS-222) during handling.

In addition to the ultrasonic tags placed on the experimental fish, plastic disk tags were affixed to the back of all fish. They were released along with 2–3 additional fish which were tagged only with a plastic disk tag. A total of eighty-six additional fish were

released in this manner.

Three types of 50 KHz ultrasonic transmitters were used during this study. A one-channel transmitter (Type MBK-450, Koden Electronic Co., Ltd.) provided depth information. Two-channel transmitters, designed by one of the authors (A. Nakamura), provided either depth and illumination or depth and temperature information. These transmitters were of similar design to those described by Ichihara et al. (1975), Nakamura (1977), and Nakamura et al. (1979), with improved electronic circuitry (Nakamura and Ishida, 1983) and mechanical structure of the depth sensor.

The receiver for the one-channel transmitter was identical to the unit described by Ichihara et al. (1972). The receiver for the two-channel transmitters was designed by one of the authors (A. Nakamura) and was described by Nakamura et al. (1979). Tracking signals from the transmitters were detectable within 2 km at sea and depth signals detected within about 600 m were recorded by the receiver. Vessel position was plotted every twenty minutes from radar bearings or by using Decca. The location of the vessel when approaching the transmitter signal was considered to be the position of the salmon being tracked.

A Straightness Index (SI) using tracking data for a fish was calculated by the formula:

$$SI = ADM/SDM$$

ADM = actual distance of movement
(total horizontal distance tracked)

SDM = straight distance of movement
(distance from initial to final tracked position)

Swimming speed was determined by recording the horizontal distance covered, which was recorded at twenty minute intervals. For calculation of swimming depth, analog records of swimming depth were read at one minute intervals. Vertical swimming speed was also determined from the analog records of the depth at one minute intervals.

Water temperature and salinity at 0 m, 5 m, 10 m, 20 m, and 30 m were monitored directly by a T-S bridge (Type MC-5, Electronic Switchgear, Ltd.). Depth was measured using an echo sounder aboard the research vessel.

Results

Horizontal movements. Patterns of horizontal

movements typical of the treatment groups are illustrated in Figs. 1-5.

Fish No. 81-10 (refer to Table 1), an intact con-

trol, exhibited horizontal zigzag movements for about three hours before approaching the coastline in the vicinity of the Abashiri River (Fig. 1). Intact

Table 1. Data for chum salmon used in tracking study, grouped by treatment, from 1979 to 1981. FL, fork length; BW, body weight; ND, nearest distance to shoreline, ADM, actual distance of movement, SDM, straight distance of movement; SI, straightness index.

Treatment of fish	Fish No.	Sex	FL (mm)	BW (g)	Capture site	Release site		Period of tracking	ADM (km)	SDM (km)	SI
						ND (km)	Water depth (m)				
Intact											
	79-1	F	660	—	Set net	7.7	55	4h 03	6.3	1.7	3.71
	79-2	F	720	—	Abashiri River	6.0	49	17h 02	17.2	4.3	4.00
	79-3	M	680	—	Abashiri River	9.1	52	10h 00	8.7	7.9	1.10
	79-4	F	780	—	Abashiri River	5.1	38	6h 27	1.7	3.6	0.47
	79-5	M	610	—	Abashiri River	6.4	40	5h 22	12.2	4.2	2.90
	79-6	M	690	—	Abashiri River	9.4	64	10h 50	42.7	3.9	10.95
	79-7	M	700	—	Abashiri River	8.3	50	8h 00	28.6	6.1	4.69
	79-8	M	590	—	Abashiri River	17.8	360<	3h 52	9.3	2.3	4.04
	79-9	F	680	—	Abashiri River	15.4	360<	15h 48	40.5	21.0	1.93
	79-10	M	550	—	Abashiri River	9.0	117	21h 33	53.7	25.8	2.08
	79-11	M	660	—	Set net	27.2	280	14h 30	78.7	26.2	3.00
	79-12	M	720	—	Set net	18.7	360<	39h 42	104.3	31.6	3.30
	80-1	M	645	3110	Set net	5.8	40	6h 38	16.1	7.5	2.15
	80-2	M	665	2910	Abashiri River	5.6	37	2h 35	4.8	4.0	1.20
	80-3	M	710	4060	Abashiri River	3.5	34	10h 28	15.2	9.8	1.55
	80-8	M	638	3360	Abashiri River	18.2	310	2h 41	8.8	7.5	1.17
	80-12	M	707	2030	Abashiri River	17.1	210	20h 03	32.4	25.8	1.26
	80-13	M	—	2960	Abashiri River	18.7	190	25h 52	44.9	20.7	2.17
	81-7	M	660	2180	Set net	5.5	45	3h 54	14.4	7.9	1.82
	81-8	F	725	4250	Set net	10.3	65	14h 43	58.6	22.4	2.62
	81-10	M	720	3910	Abashiri River	5.9	38	7h 58	19.9	6.1	3.26
	average							12h 00	29.5	11.9	2.83
Sham operation											
	80-9	M	724	4110	Abashiri River	5.0	40	16h 39	16.6	5.6	2.96
Visual ablation											
	80-6	M	665	3610	Abashiri River	3.9	43	11h 35	24.6	7.5	3.28
	80-14	M	595	2960	Abashiri River	4.0	36	4h 57	6.8	3.7	1.84
	81-1	F	670	4110	Abashiri River	5.6	40	24h 41	55.5	7.1	7.82
	81-4	M	700	4910	Abashiri River	6.4	36	9h 23	14.5	6.8	2.13
	81-6	M	690	3700	Abashiri River	6.5	36	2h 06	5.9	2.6	2.27
	81-9	M	700	3810	Abashiri River	6.5	42	7h 31	19.9	5.3	3.75
	average							10h 02	21.2	5.5	3.52
Olfactory ablation											
Cut											
	80-4	M	710	4080	Abashiri River	3.6	34	5h 20	12.7	6.1	2.08
	80-5	M	648	3210	Abashiri River	3.3	34	6h 16	16.7	11.7	1.43
	80-7	M	615	2610	Abashiri River	7.6	50	24h 35	46.4	5.7	8.14
	average							12h 02	25.3	7.8	3.88
Wax											
	80-11	M	—	4110	Abashiri River	5.1	38	7h 53	11.1	4.3	2.58
	81-2	F	672	3700	Abashiri River	5.7	36	3h 04	8.3	4.2	1.96
	81-3	M	680	4410	Abashiri River	5.6	36	9h 23	26.7	4.9	5.45
	81-5	M	635	2960	Abashiri River	6.7	37	6h 39	11.5	7.7	1.49
	average							6h 45	14.4	5.3	2.87
	(average of cut and wax combined)							(9h 01)	(19.1)	(6.4)	(3.30)
Visual and olfactory ablation											
	80-10	M	705	3910	Abashiri River	7.5	48	9h 40	11.8	1.0	11.80

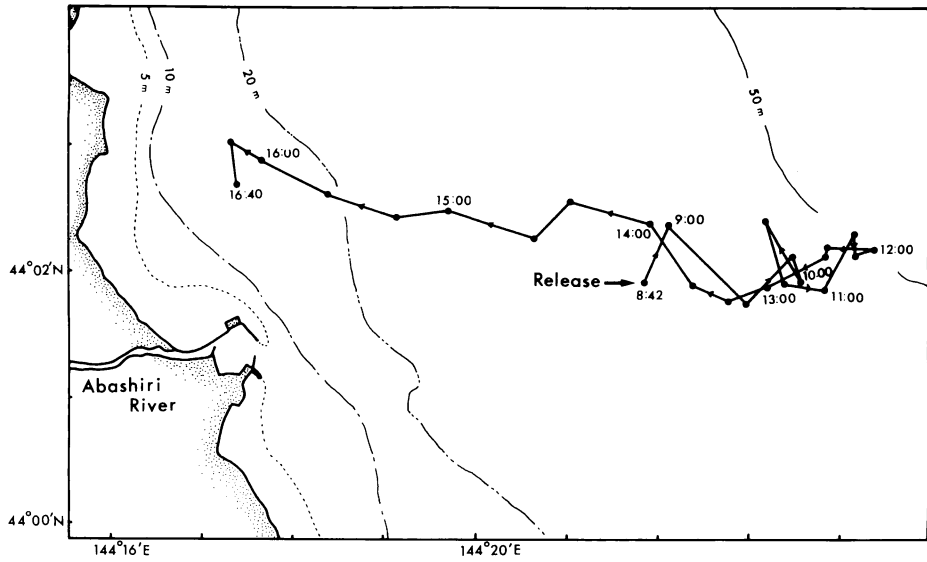


Fig. 1. Horizontal movements of intact chum salmon, fish No. 81-10.

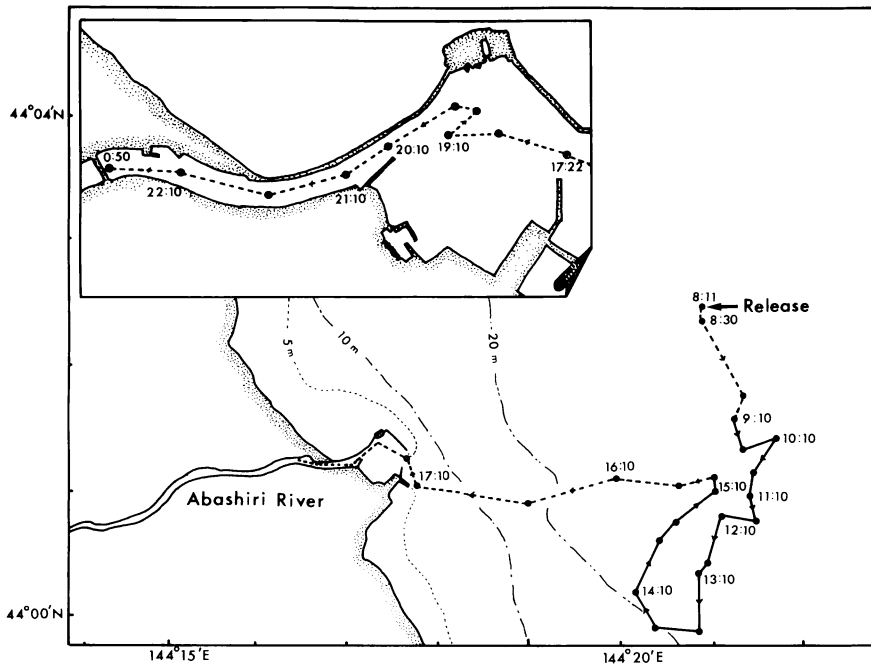


Fig. 2. Horizontal movements of chum salmon receiving a sham olfactory operation, fish No. 80-9. Inset shows tracking while in the Abashiri River; solid line denotes tracking during flood tide, dotted line indicates tracking during ebb tide.

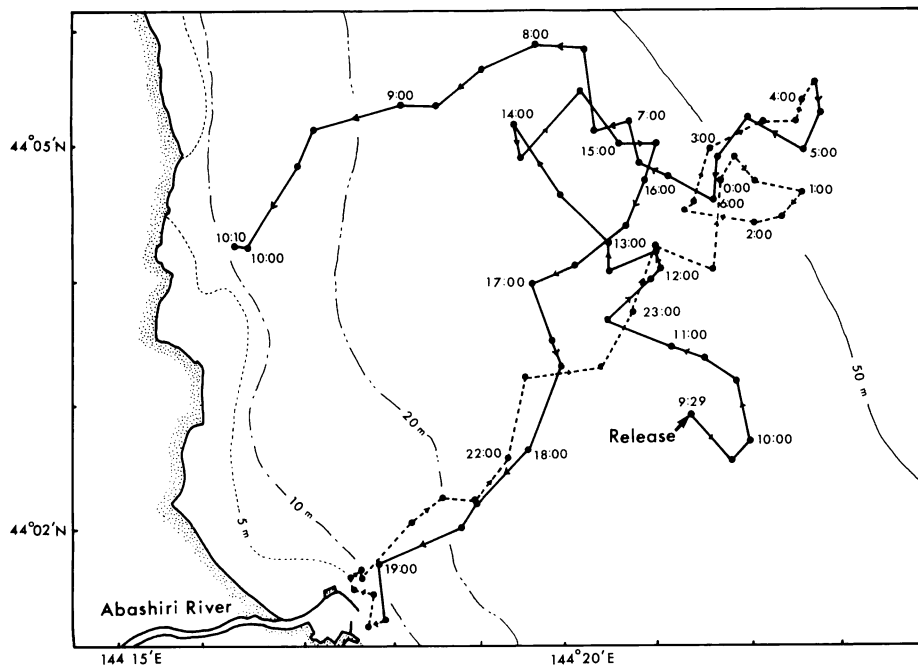


Fig. 3. Horizontal movements of chum salmon subjected to visual ablation, fish No. 81-1. Solid line denotes tracking during flood tide, dotted line indicates tracking during ebb tide.

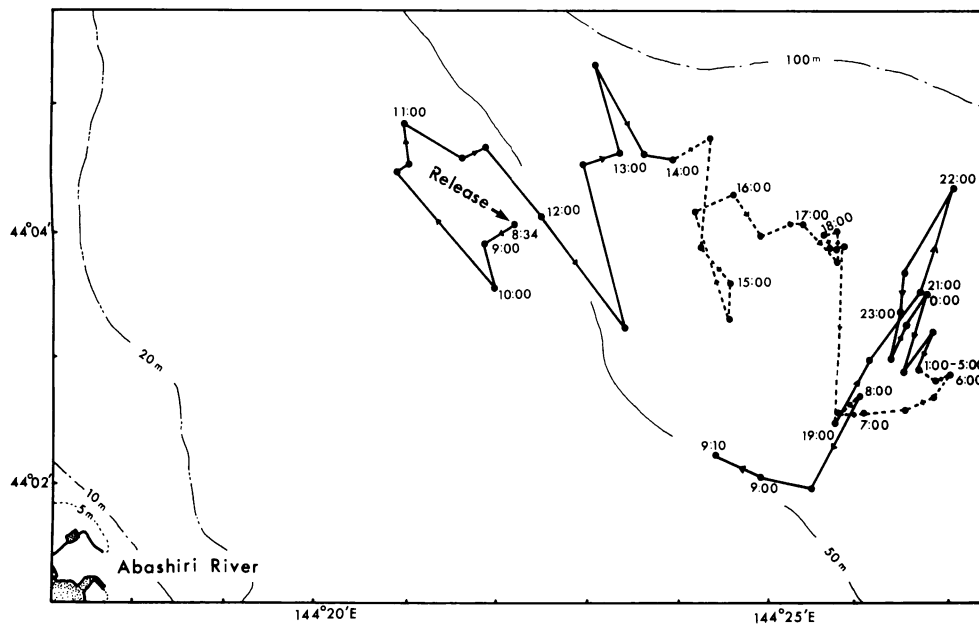


Fig. 4. Horizontal movements of chum salmon receiving olfactory ablation, fish No. 80-7. Solid line denotes tracking during flood tide, dotted line indicates tracking during ebb tide.

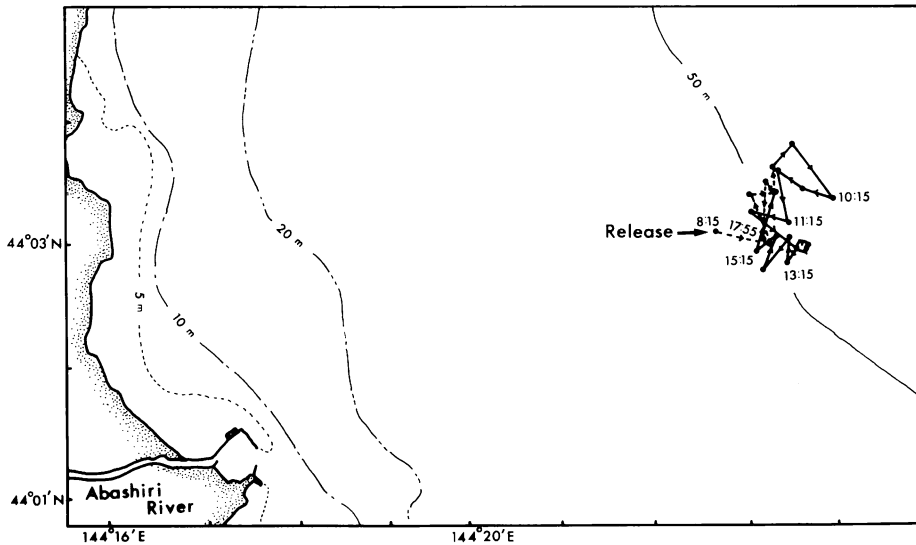


Fig. 5. Horizontal movements of chum salmon receiving both visual and olfactory ablation, fish No. 80-10. Solid line denotes tracking during flood tide, dotted line indicates tracking during ebb tide.

fish did not usually remain in a restricted area after release and had an overall average SI of 2.83.

A sham operated fish (fish No. 80-9) migrated most directly towards mouth of the Abashiri River, showing limited zigzag movements (Fig. 2). This was the only experimental fish which entered the river during the tracking period. After remaining at the mouth of the river for about three hours, the fish ascended the stream during the ebb tide. The SI for this fish was 2.96.

Tracking movements for fish No. 81-1, with vision blocked, were recorded over three tidal cycles (Fig. 3). The fish swam in a zigzag pattern following release and migrated towards the mouth of the river during flood tide. Although the fish arrived very near the mouth of the river, it did not enter, swimming offshore during the ebb tide, and returning to the coast during the following flood tide. Average SI for all of the visually deprived fish was 3.52.

Olfactory ablation, illustrated by fish No. 80-7, caused fish to swim in a continuous zigzag pattern, exhibiting no directed coastward migration (Fig. 4). The fish remained in a restricted area during tracking. Average SI for these fish was 3.30.

Fish No. 80-10, having both senses removed, moved in a very restricted area, exhibiting a tight zigzag pattern (Fig. 5). The SI for this fish was 11.8.

Swimming speed. The average and maximum swimming speeds for experimental fish are given in

Table 2. Daylight swimming speeds were faster than night speeds for all groups, except the intact fish group in 1981. Swimming speeds of intact fish were higher than in any of the other groups.

In all groups, vertical swimming speed was found to be nearly the same for both upward and downward rates during day and night periods (Table 3). Generally, average swimming speed for intact fish was faster than in all other treatment groups both during the day and at night.

Vertical movements. Patterns of vertical movements exhibited by the experimental fish are shown in Figs. 6-10.

Intact fish, No. 81-8, swam downward rapidly following release from the vessel. Remaining near the bottom for a time, it ascended to the surface layer and swam downward and upward in a fairly regular pattern (Fig. 6). Other fish with intact senses showed approximately the same pattern of amplitude and regularity.

Vertical movements of sham operated fish, No. 80-9, were similar to those of intact fish, following release from the vessel. After ascending to the surface layer, it also swam downward and upward (Fig. 7). However, the peaks of upward movements did not reach the surface layer until 15:30, several hours later than for intact fish. At 17:22 the fish entered the mouth of the Abashiri River and swam mainly in the surface layer.

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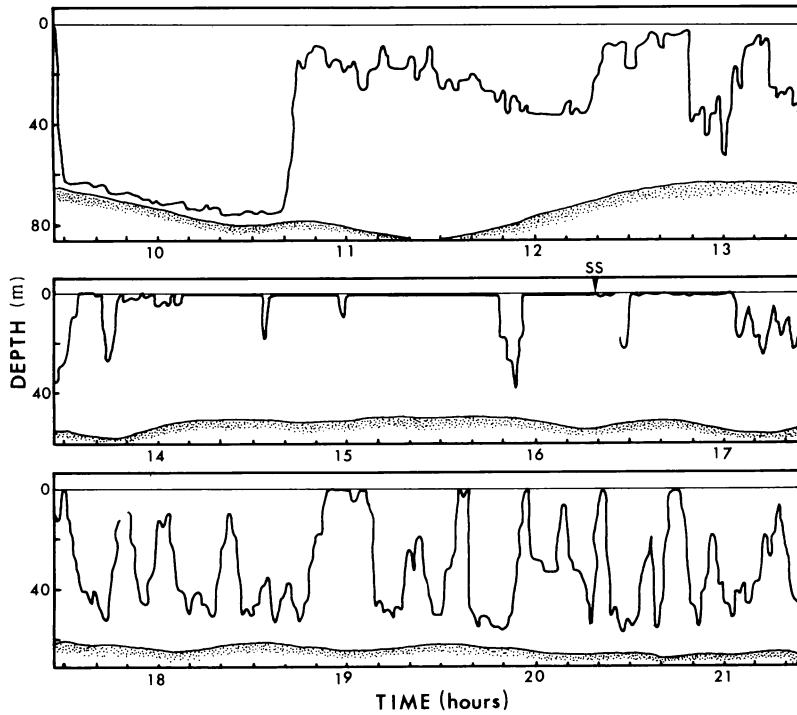


Fig. 6. Vertical movements of intact chum salmon, fish No. 81-8.

Table 2. Average and maximum swimming speeds for experimental chum salmon from 1979 to 1981. RFL/S (rate of FL/sec) = distance of movement per one second (cm)/fork length (FL, cm) in each fish.

Treatment of fish	Year	Daytime				Nighttime				
		cm/sec	RFL/S	max. (cm/sec)	n	cm/sec	RFL/S	max. (cm/sec)	n	
Intact	1979	78.9	1.26	390.0	238	77.9	1.16	416.7	185	
	1980	74.9	1.13	250.0	125	43.4	0.64	149.3	78	
	1981	80.4	1.23	314.2	56	97.9	1.40	411.7	22	
	\bar{x}	80.4	1.21	318.1	—	73.1	1.07	325.9	—	
Sham operation	1980	48.0	0.67	120.3	25	32.8	0.46	50.3	3	
Visual ablation	1980	45.8	0.72	114.7	50	—	—	—	—	
	1981	57.6	0.84	176.5	82	57.6	0.84	164.2	44	
	\bar{x}	51.7	0.78	145.6	—	—	—	—	—	
Olfactory ablation	Cut	1980	65.6	1.00	201.7	73	36.5	0.59	200.8	37
		Wax	1980	47.3	0.71	120.7	24	—	—	—
	\bar{x}	1981	59.1	0.89	203.8	53	26.3	0.39	90.7	34
		\bar{x}	57.3	0.86	175.4	—	31.4	0.49	145.8	—
Visual and olfactory ablation	1980	39.2	0.55	88.8	29	—	—	—	—	

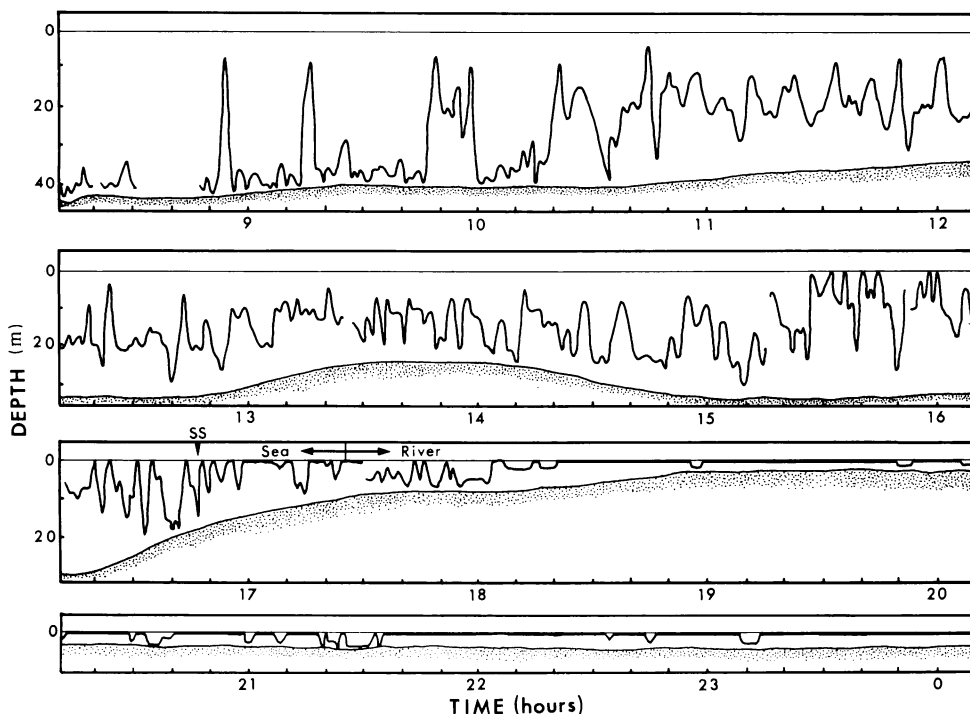


Fig. 7. Vertical movements of chum salmon receiving a sham olfactory operation, fish No. 80-9. SS: sunset.

Fish No. 81-1, whose sight was obliterated, favored mid-water at depths of 10–30m following release, and exhibited a regular upward and downward pattern (Fig. 8). All visually deprived fish showed this pattern and generally did not return to the surface.

The typical upward and downward pattern exhibited by the other groups was not seen in fish with olfactory ablation. Fish No. 80-7 showed some vertical swimming movement for about three hours following release, then remained mostly in the sur-

face layer (Fig. 9). Some of the other fish with olfaction blocked tended towards the bottom after briefly showing some vertical movement.

When both sight and smell were removed, fish No. 81-10 exhibited very little upward and downward swimming. Swimming tended to be in the surface layer or near the bottom (Fig. 10). Vertical swimming for this fish was similar to that of the fish with olfactory ablation.

Swimming depth. Frequency distributions of swimming depth taken at one minute intervals for each of the treatment groups are shown in Fig. 11. Intact fish swam most frequently within 0–5 m level. The sham operated fish had high frequencies at 0–5 m and 15–20 m. Visually deprived fish usually remained midwater with a peak frequency at 15–20 m. Fish having ablated olfaction showed one mode at 0–5 m and another at 35–40 m. Removal of both sight and smell showed a high frequency at 0–5 m, and smaller modes at 15–20 m and 55–60 m. These two groups showed essentially the same pattern.

Frequency distributions of swimming depths from 0–80 m by 10 m intervals were statistically examined for differences between the groups. A chi-square test rejected the null hypothesis that the swimming depth

Table 3. Average upward and downward swimming speeds of experimental chum salmon from 1979 to 1981. USS, upward swimming speed (cm/sec); DDS, downward swimming speed (cm/sec).

Treatment of fish	Daytime		Nighttime	
	USS	DSS	USS	DSS
Intact	7.8	7.3	11.0	10.5
Sham operation	7.1	7.3	5.0	4.0
Visual ablation	5.5	6.0	4.2	4.5
Olfactory ablation	5.3	5.5	5.3	6.2
Visual and olfactory ablation	3.8	5.0	—	—

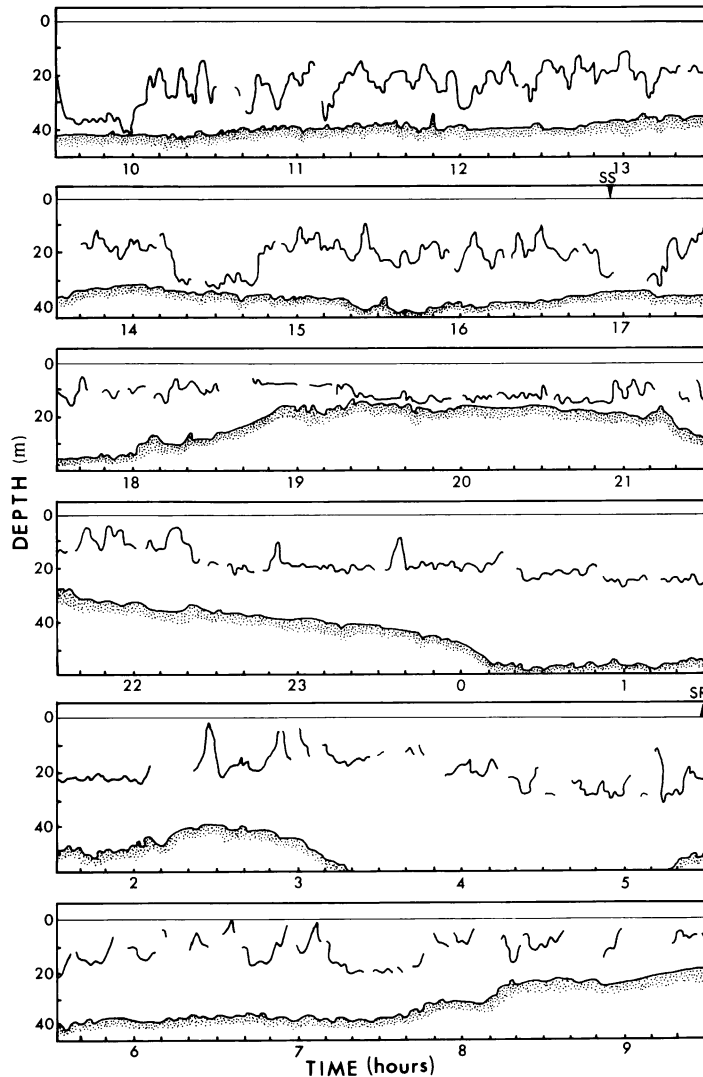


Fig. 8. Vertical movements of chum salmon subjected to visual ablation, fish No. 81-1. SS: sunset, SR: sunrise.

of intact fish were the same as the fish with visual, olfactory or both senses obliterated at the 1% significance level. This clearly indicates that intact fish occupied different swimming depths than fish experiencing some sensory deprivation.

Tag recovery. In tracking experiments, 124 fish (including 36 both transmitter and tag attached fish) were tagged and released from 1979 to 1981. Intact fish numbered 107, eight fish were visually deprived, seven fish had their olfaction ablated, one fish had both senses obliterated, and one fish received the

sham operation. For intact fish, 36.4% were recaptured in the Abashiri River and 33.6% were taken at sea by the set net sites (recapture was 70.0% of released fish). Fish with vision ablated had 37.5% recaptured in the Abashiri River and 25.0% taken by the set nets (62.5%). Fish experiencing olfactory ablation showed 71.4% recaptured with the set nets (71.4%).

Daily movement for each of the groups from tag recovery data is presented in Table 4. Intact fish captured in the Abashiri River showed a lower av-

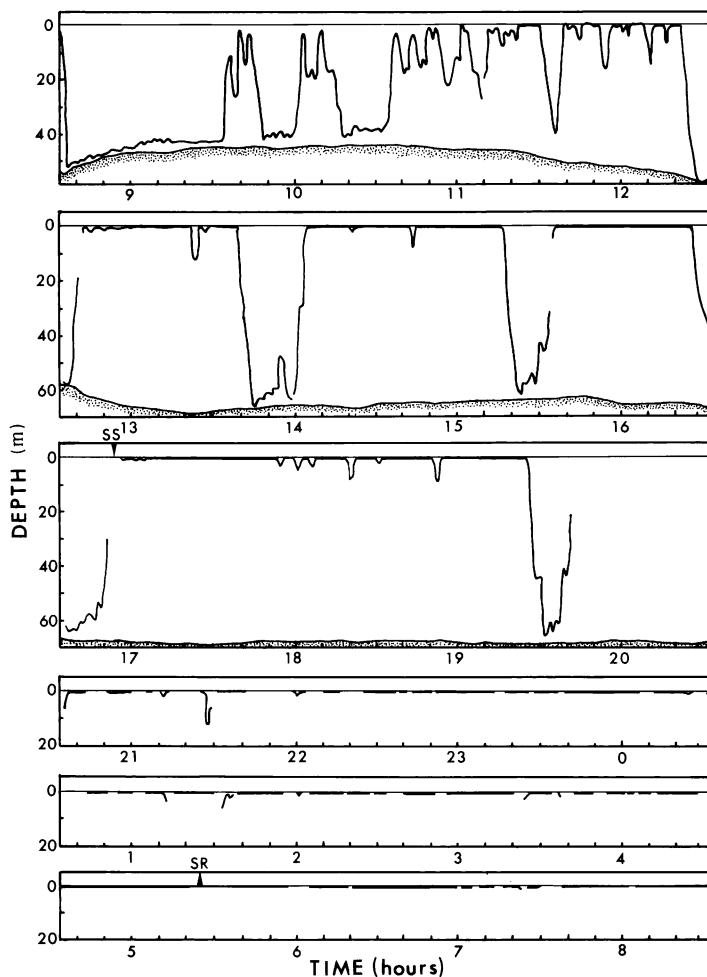


Fig. 9. Vertical movements of chum salmon receiving olfactory ablation, fish No. 80-7. SS: sunset, SR: sunrise.

erage distance of movement than the intact fish captured at the set net sites (3.50 km/day vs 7.45 km/day). Fish deprived of vision or olfaction showed lower values, indicating a faster rate of movement in fish left intact.

Temperature and salinity. Water temperature and salinity measurements were made while conducting the tracking observations during flood and ebb tides. In 1980, data were collected at 57 stations during flood tide and 50 stations during ebb tide, while in 1981, measurements were taken at 22 stations during flood and 11 stations during ebb.

Isohalines of surface waters during flood tides from 1981 data are presented in Fig. 12 and show the influence of flushing of the Abashiri River waters on

the adjacent ocean. At stations A and B, low salinities (19.00‰ and 22.00‰) were found only at the surface. Salinities at 5 m and 10 m did not differ from other stations (Table 5). The effect of the Abashiri River was observed during both years and during flood and ebb tides.

Discussion

In a tagging study of sockeye salmon by Craigie (1929), he stated that the elimination of olfactory sensibility appears definitely to interfere to some extent with the migration of the salmon, but whether by removing guiding impulses or in some less direct way is not clear. The olfactory hypothesis for

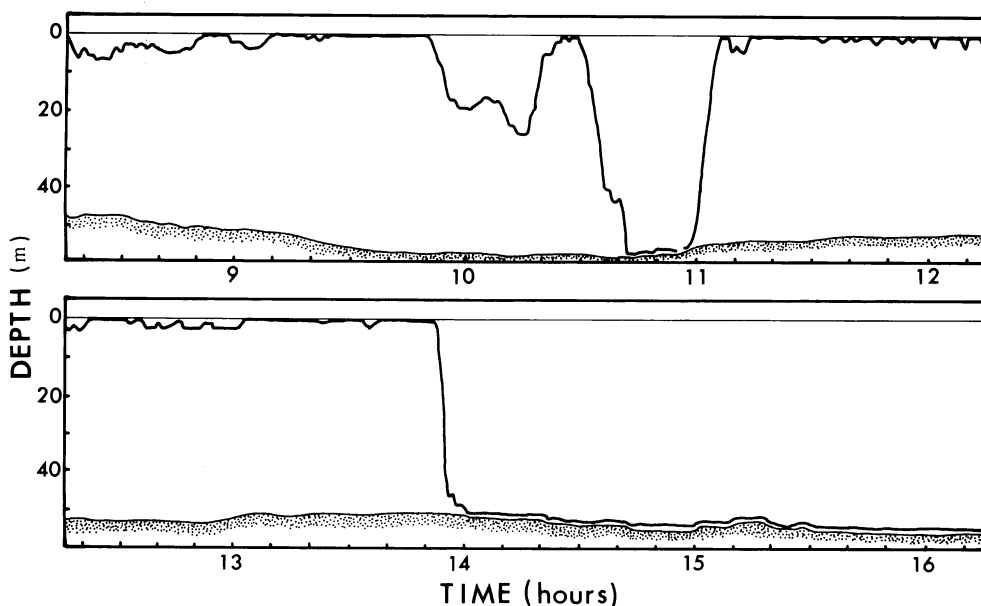


Fig. 10. Vertical movements of chum salmon receiving both visual and olfactory ablation, fish No. 80-10.

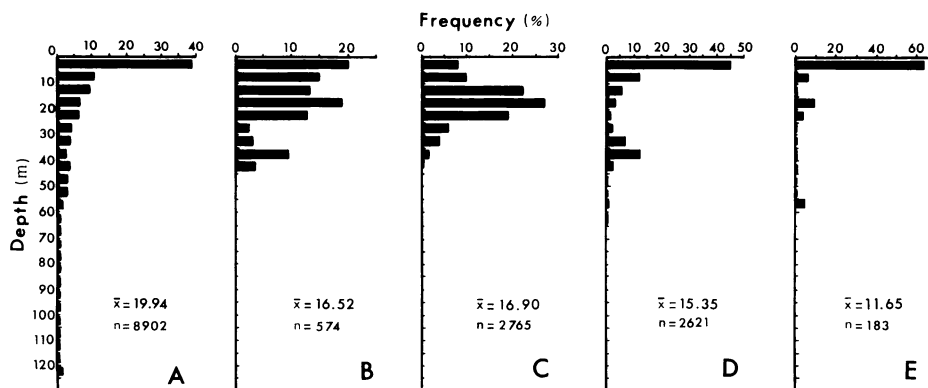


Fig. 11. Frequency distribution of swimming depth for treatment groups of chum salmon. A: intact, B: sham operation, C: visual ablation, D: olfactory ablation, E: both visual and olfactory ablation, \bar{x} : average.

salmon homing, first presented by Hasler and Wisby in 1951, has three basic tenets: 1) each stream has a unique chemical composition and a distinctive odor; 2) before juvenile salmon migrate to the sea, they become imprinted to the distinctive odor of their home stream; 3) adult salmon use this information as a cue for homing. Sensory impairment experiments have been used to test this hypothesis in 20 studies, and olfaction was shown to be necessary for correct homing in 16 of these experiments (Hasler and Scholz, 1983). Hiyama et al. (1966) and Groves et

al. (1968) demonstrated that blinded fish homed nearly as well as control fish, indicating that vision was not essential for locating the original stream, at least during the upstream migration. Electrophysiological studies have also suggested that salmon can distinguish their home water from other water (Hara et al., 1967; Ueda et al., 1967). Solomon (1973) postulated that metabolic products or race-specific pheromones may be responsible for the homing of Atlantic salmon, and Nordeng (1971, 1977) presented a similar hypothesis for migratory salmonids.

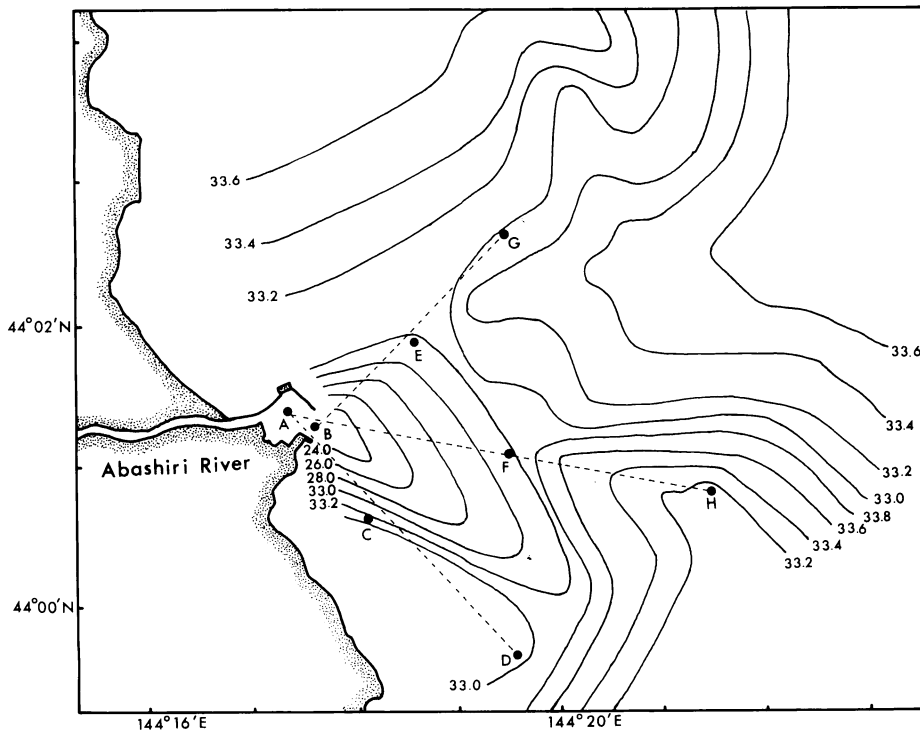


Fig. 12. Isohalines of surface waters during flood tide off the Abashiri River in 1981. Values for stations are given in Table 5.

In our tagging study, intact fish and fish with their vision ablated returned to the home river, but fish subjected to olfactory ablation did not. This confirmed that olfaction was necessary for correct choice of home streams as shown in previous studies.

There were differences observed in the behavior of intact *and* ablated fish. In horizontal movements, visual and olfactory ablation caused the fish to swim in a more limited horizontal zigzag pattern than fish left intact or receiving a sham operation. Perhaps the limited movement of fish receiving olfactory ablation was the result of being unable to sense the

home river.

Both the intact and sham operated fish swam in horizontal zigzag patterns, suggesting that selection of water masses is facilitated by this movement, as concluded by Johnsen and Hasler (1980) and Johnsen (1981). Jamon (1990) reported that the last stage in open-sea migration, in which Pacific salmon return toward their home stream mouth, is formalized as a random search model.

In a tagging study, the average daily movement of chum salmon was 25.5 km (Yonemori et al., 1975), and 38.0 km (Neave et al., 1976). Net travel rates of

Table 4. Average daily distance of movement of chum salmon based on tag recovery data from 1979 to 1981.

Treatment of fish	Recapture site	km/day	Range (km/day)	n
Intact	Abashiri River	3.50	0.3- 8.5	39
	Set nets	7.45	1.6-29.1	36
	Overall	5.39	0.3-29.1	75
Visual ablation	Abashiri River	2.03	1.4- 2.7	3
	Set nets	2.85	2.2- 3.5	2
	Overall	2.36	1.4- 3.5	5
Olfactory ablation	Set nets	2.82	0.1- 5.0	5

maturing chum salmon at sea are generally faster than those in coastal waters (Neave et al., 1976). These are much longer distances than reported by our study, perhaps due to proximity of our release sites to the coastline compared to the sites of Yonemori et al. (1975) and Neave et al. (1976). The daily distance of migration of chum salmon was estimated by tagging study in the coastline and these estimates were lower than the results for mature chum salmon in offshore areas (Ueno, 1991). In point-to-point tag recovery data, the daily distance of migration of chum salmon in coastal waters may be less than the daily distance of migration in offshore areas due to active horizontal zigzag movements observed in this study in the coastal waters to sense the water masses and locate the correct tributary. Quinn (1990) reported that the difference between offshore and coastline movements is partially attributable to salmon delaying off the mouths of streams as they mature or prepare for the transition between salt and fresh water. In this study, after remaining at the mouth of the river for about three hours, the salmon ascended the stream.

The swimming speed of the intact fish was clearly faster than for fish with their senses blocked. In other studies, the average swimming speeds for chum salmon monitored by ultrasonic telemetry were 72.0 m/min (120 cm/sec) during daylight and 76.5 m/min (127.5 cm/sec) at night (experiments off Etorofu Island) by Ichihara et al. (1975); 55.2 m/min (92.0 cm/sec) and 66.6 m/min (111.0 cm/sec) (off Shiretoko) by Yoza et al. (1985); 31.2 m/min (52.0 cm/sec) and 42.0 m/min (70.0 cm/sec) (off Abashiri) by Shimamura et al. (1987); and 28.5 m/min (47.5 cm/sec) in 1984 and 21.1 m/min (35.2 cm/sec) in 1985 (off Sanriku) by Ishida et al. (1988). The average swimming speed for intact fish in this study was equal to or less than the speeds reported in the above studies.

The patterns of vertical movements for chum salmon in this study are presented in Fig. 13. Intact fish and fish receiving the sham operation moved vertically with a regular amplitude. We conclude that homing salmon move to the surface to detect home water after refreshing their nostrils in deeper water. Regular vertical movement would be effective in refreshing olfactory epithelia which might become acclimated when exposed to one odor.

Fish subjected to visual ablation tended towards midwater and exhibited a regular vertical amplitude, but did not come to the surface. This suggests that

vision is an important sense for regulating the amplitude of vertical movements. Based on the predominantly daytime movements of steelhead trout in coastal waters, it was suggested that the sun and polarized light might be involved in orientation (Ruggerone et al., 1990).

The vertical movements of fish experiencing olfactory ablation can be divided into two types. Following release, fish of both types moved upward and downward, but later some fish swam in the surface layer (Type I in Fig. 13), while others swam near the bottom (Type II in Fig. 13). Yano et al. (1984) observed that upon encountering Dall's porpoise, chum salmon tended to either dive straight down to the bottom or to remain swimming around in the surface. These type movements may be sometimes caused by the effects of other primary factors.

The vertical movements of fish with both visual and olfactory ablation were observed to be similar to Type II mentioned above. It appears that for these fish, the vertical movements were more similar to those having only olfactory ablation than those with visual ablation. Ichihara et al. (1975), Soeda et al. (1985), and Shimamura et al. (1987) reported that active upward and downward movements of chum salmon were observed by ultrasonic telemetry. Ichihara et al. (1975) and Ichihara and Nakamura (1980) suggested that the characteristic vertical movements were probably related to the olfactory sense.

Westerberg (1982), in ultrasonic tracking studies, reported that movement was closely related to the fine-scale layering of the water. In 1984, Westerberg suggested that vertically stratified hydrographic fea-

Table 5. Water temperature and salinity measurements at eight stations in the mouth of the Abashiri River and directly offshore. Station letters refer to locations listed in Fig. 12.

St.	Temperature (°C)			Salinity (‰)		
	0 m	5 m	10 m	0 m	5 m	10 m
A	17.0	16.7	—	19.00	33.30	—
B	16.9	16.8	16.8	22.00	33.32	33.34
C	17.4	16.8	16.7	33.20	33.29	33.33
D	17.0	16.7	16.7	33.09	33.33	33.36
E	16.8	16.6	16.6	33.15	33.31	33.36
F	16.9	16.6	16.6	32.78	33.29	33.35
G	13.4	13.3	13.3	32.93	32.93	32.95
H	17.1	16.5	16.5	33.17	33.38	33.39

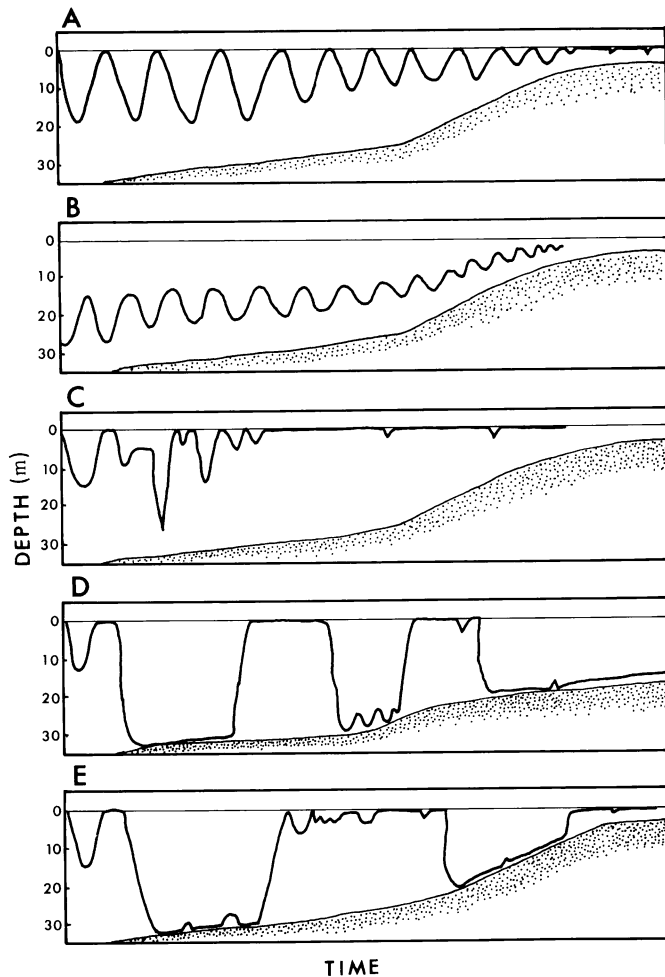


Fig. 13. Generalized patterns of vertical movements for chum salmon according to experimental treatment. A: intact and sham operation, B: visual ablation, C: olfactory ablation Type I, D: olfactory ablation Type II, E: both visual and olfactory ablation.

tures may be important for the salmon's orienting movements. Quinn and terHart (1987) reported that sockeye salmon were tracked in three distinct oceanographic regimes: cold, saline, weakly stratified waters; less saline, vertically well-mixed waters; and warm, relatively fresh, strongly stratified waters, and that the salmon had a general preference for near-surface water, as evidenced by their shallow distribution in the mixed region. Ruggerone et al. (1990) reported that steelhead trout may obtain directional information from the odor concentration above and below the halocline. Døving et al. (1985) reported, using electrophysiology, that 90% of responding neurons showed differential response to water sam-

ples from different depths. They concluded that olfactory discrimination of fine-scale hydrographic features may provide a necessary reference system for successful orientation in near shore regions by salmon.

An interesting similarity to the vertical zigzag movements can be found in the horizontal zigzag movements in coastal and near shore migrations, as well as in the stream phase of homing. The zigzag movements, both horizontal and vertical, allow the fish to sense the water masses and locate the correct tributary.

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視覚および嗅覚の喪失が母川回帰中のシロザケの遊泳行動に与える影響とそれら感覚器官の母川探索における重要性

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1979年から1981年の3年間にオホーツク海の北海道沿岸で、バイオテレメトリー手法を用いて母川回帰直前のシロザケの遊泳行動に関する研究を行った。36尾のシロザケでテレメトリーを用いた調査を行い、このうち21尾は正常魚であり、6尾は視覚を、7尾は嗅覚をそれぞれ喪失させた。1尾は視覚と嗅覚の両方を喪失させた。また、1尾は嗅索は切断せずに外傷のみを与えた。これら追跡に用いたサケのうち、網走川上流のサケ、マスふ化場で捕獲された30尾のものは網走川起源のサケであると考え

られたが、定置網で捕獲された6尾のものの河川の起源については不明であった。視覚あるいは嗅覚を喪失させた魚は、正常魚あるいは外傷魚よりも狭い範囲内で水平ジグザグ遊泳行動が見られた。直線指数【SI=全追跡距離(ADM)/追跡開始地点と追跡終了地点の直線距離(SDM)】は、視覚および嗅覚喪失魚が正常魚および外傷魚よりも高かった。水平および垂直移動速度は、正常魚が視覚および嗅覚の喪失魚よりも速かった。水面と海底近くで行われる規則正しい垂直遊泳行動は、正常魚と外傷魚で見られた。視覚喪失魚は、中層域で正常魚と同じ様な規則正しい垂直遊泳行動が見られたが、その行動の多くは水面付近までは上昇してこなかった。嗅覚喪失魚は、規則正しい垂直遊泳行動が見られず、水面付近あるいは海底付近を遊泳していた。正常魚の規則正しい垂直遊泳行動は、河川水の影響を受ける表層水での河川の臭いに関する情報について嗅覚の慣れが起きないようにするため、深層水でこれらの表層河川水の臭いを洗い流すことにより、母川の探索を容易にすることが推察された。またさらに、視覚を用いることにより水面付近への移動が容易になるものと考えられた。以上の結果より、シロザケの母川回帰のためには、嗅覚を用いた母川の臭い物質の探索が直接的には重要であるが、これに加えて嗅覚や視覚の感覚器官を利用した水平および垂直のジグザグ遊泳行動も母川探索のためには重要な役割を持つことが考えられた。

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