MOVEMENTS AND HOMING OF CUTTHROAT TROUT (*SALMO CLARKI*) FROM OPEN-WATER AREAS OF YELLOWSTONE LAKE

by

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Vita

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ABSTRACT

Cutthroat trout (*Salmo clarki*) showed in-season homing after displacement from their spawning tributaries to Yellowstone Lake during June-August, 1966 and 1967. Of 475 trout tagged and displaced from Clear and Cub creeks to three release points (0.5-22.0 km) in the lake and to the mouth of Clear Creek, 32.4% homed, 7.6% strayed, 2.5% were caught by anglers, and the remaining were unaccounted for. Anosmic and blind-anosmic fish homed in significantly fewer numbers than other groups. Fish released just outside the mouth of the homestream had the shortest average homing time, but the average homing time for fish displaced 22.0 km from the homestream was shorter than those displaced 5.0 km away. Homing percentages for trout tagged after tracking were similar and average homing times longer than for those used in group tagging experiments. Orientations in the direction between northeast and southeast generally occurred for most fish tracked in open-water and were related to sun azimuth and current. Fish taken from the east side of the lake went west-northwest when tracked late in the afternoon and fish taken from the west side of the lake went east-southeast when tracked in the morning. The directions of orientation were generally toward the homestreams and sun azimuths. Mean directions for males and females were generally not significantly different. Average swimming speeds and vector lengths for males and females were about the same. Immature cutthroat trout could be trained to use a light source as a reference point for orientation.

Movements and Homing of Cutthroat Trout (*Salmo clarki*) from Open-Water Areas of Yellowstone Lake

INTRODUCTION

Open-water movements and in-season homing of mature cutthroat trout (*Salmo clarki*) after displacement from spawning streams of Yellowstone Lake, Wyoming were studied during the trout spawning seasons (May to August) of 1966 and 1967. Yellowstone Lake has a surface area of 354 km^2, maximum depth of 98 m, mean depth of 42 m, and is at an altitude of 2,358 m (Benson, 1961). It is a good place for homing and movement studies because of its relatively large size and numerous spawning tributaries, and because the cutthroat trout population is not contaminated with salmonids from other sources. The objectives were to compare open-water orientation of cutthroat trout taken from Clear, Cub, Pelican and Arnica creeks, and to compare the homing performance of those from Clear and Cub creeks. In addition, underwater photographs were made in an attempt to ascertain if landmarks were visible to the fish. Laboratory experiments were conducted to determine if cutthroat trout could be trained to use light for orientation.

In-season homing of mature cutthroat trout in Yellowstone Lake was observed by McCleave (1967) who displaced 1908 trout and found that 32.2% homed, 6.2% strayed, and 1.5% were caught by anglers. Platts (1959) showed in-season homing for cutthroat trout displaced in a Utah reservoir after spawn was taken.

Natal homing studies by Ball in Yellowstone Lake (1955) showed that cutthroat trout marked at age I had a strong tendency to return to the parent stream as adults at age III or IV. Cope (1957) found that 97% of the repeat spawners in Yellowstone Lake homed and suggested that each stream has its own race of cutthroat trout.

In-season homing of sockeye salmon (Oncorhynchus nerka) and pink salmon (O. gorbusha) was observed by Hartman and Raleigh (1964) and Helle (1966), respectively. Natal homing of salmon was reported by Clemens et al. (1939), Donaldson and Allen (1957), Jones (1959), and reviewed by Hasler (1966). Natal and repeat homing for brown trout (Salmo trutta) were observed by Stuart (1957) and for rainbow trout (Salmo gairdneri) by Lindsey et al. (1959). In-season and repeat homing for char (Salvelinus willughbii) were shown by Frost (1963).

Previous studies on open-water movements of cutthroat trout showed that orientation was mainly eastward and northward from various release points in Yellowstone Lake (Jahn, 1966; McCleave, 1967). This was also true for blind and anosmic trout which oriented as well as control trout. However, orientation was generally not toward the home stream. A southward shift in mean direction was noted for trout tracked after noon (Jahn, 1966). The sun may have served as a reference point in orientation since trout traveled farther and showed a stronger tendency to go shoreward from a near-shore release point on sunny days than on cloudy days.

Fish other than cutthroat trout which use celestial cues for orientation include young sockeye salmon (Groot, 1965), white bass (Hasler et al., 1958), green sunfish (Schwassmann, 1960; Hasler and Schwassmann, 1960), cichlids (Braemer and Schwassmann, 1963; Hasler and Schwassmann, 1960), and parrot fishes (Winn et al., 1964).

Cues suggested for detection of the home stream by fish include temperature (Ward, 1921), carbon dioxide (Powers, 1939; Powers and Clark, 1943; Collins, 1952), gradients of inorganic compounds (Hasler, 1966), milt (White, 1934), and characteristic stream odor (Hasler and Wisby, 1951). The latter is the most generally accepted explanation for detecting the home stream. Attempts to explain movements include: sun-compass orientation (Hasler et al., 1958), celestial navigation (Adler, 1963), inertial guidance (Barlow, 1964), polarized light (Groot, 1965), and random movement (Saila and Shappy, 1963; Patten, 1964). Hasler (1966) discussed the significance of these.

Underwater photographs of the sun (Henderson, MS, 1963) showed many images of the sun due to small waves on the lake's surface. He stated that these multiple images may be an advantage for orientation.

Training experiments by Hasler et al., (1958) and Braemer (1960) showed centrarchids to possess a sun-compass mechanism. Other experiments demonstrated the importance of the altitude and azimuth of the sun for orientation of sunfish and cichlids (Hasler and Schwassmann, 1960; Schwassmann and Hasler, 1964).

METHODS AND MATERIALS

Release points 1, 2, 3, and 4 (Fig. 1) were used for homing studies. These were located at the mouth of Clear Creek, 0.5 km west-northwest, 5.0 km west, and 22.0 km west-southwest of the mouth, respectively. Travel time to release point 1 was 2-3 minutes, to point 2 was 3-15 minutes, to point 3 was 8-18 minutes, and to point 4 was 30-35 minutes, depending on where experimental fish were obtained and speed of the boat. Fish used in homing studies were moving upstream to spawn and were taken from traps on Clear and Cub creeks, located 75 and 150 m, respectively, above their mouths.

Homing experiments were carried out from June 29 to July 9, 1966, and July 11 to 18, 1967. A group of 25-30 trout were netted from the trap and were taken to the boat. In a few instances, fish taken from Clear Creek were carried directly to release point 1. Four types of experimental fish were used: blind-anosmic, anosmic, control and non-anesthetized. Blind-anosmic, anosmic and control fish were anesthetized in a 40 mg/liter solution of tricaine methanesulfonate (M.S. 222, Sandoz Pharmaceuticals). Fish were blinded by injecting 0.01-0.15 cm^3 of 3% aqueous benzethonium chloride (Phemerol, Parke, Davis and Co.) into their eyeballs with a syringe (McCleave, 1967). A jet of air was blown into the olfactory chambers to free them of foreign material and then petroleum jelly (Vaseline, Chesebrough-Ponds Mfg. Co.) was injected into them with a needleless syringe, until the accessory chamber anterior to the eye was full. An empty syringe was placed against the nares of control fish. Anesthetized

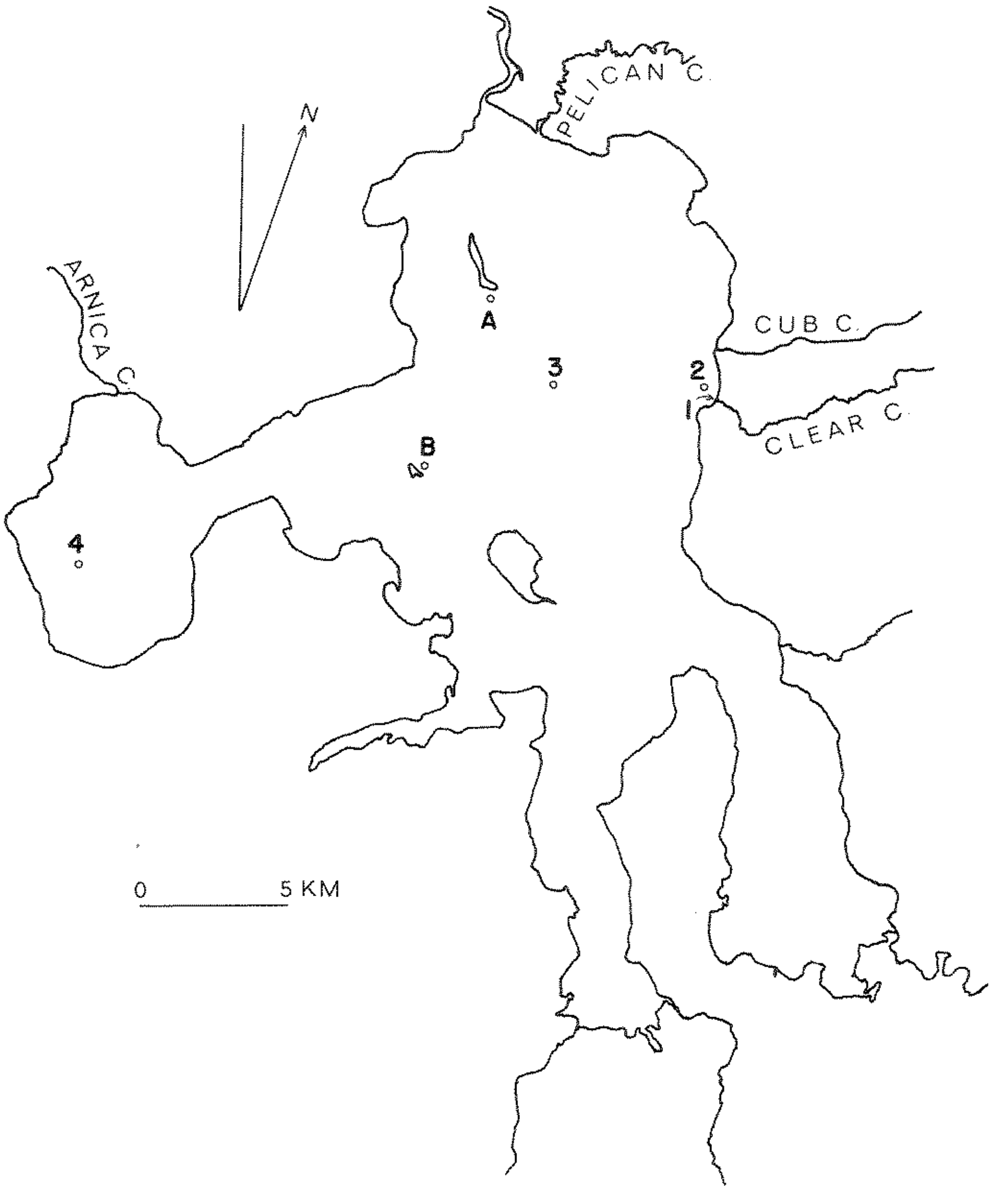

Fig. 1. Map of Yellowstone Lake showing release points and locations where experimental cutthroat trout were obtained. 1, 2, 3, 4 - release points; A, B - locations where non-spawning and spawned-out trout were captured.

fish were then tagged, placed into the stock tank, carried to the release point and liberated after recovering from the anesthetic, which was usually by the time the release point was reached.

Non-anesthetized fish were either put into a covered stock tank in the boat, carried to a release point, marked with a numbered alligator clip tag (McCleave et al., 1967) and released, or marked and released at point 1. Groups of 25 fish were tagged and liberated at each release point. A total of 50 fish from Clear Creek were released at point 1, 50 from Clear Creek and 50 from Cub Creek at point 2, 225 from Clear Creek and 50 from Cub Creek at point 3, and 50 from Clear Creek at point 4.

Most recaptures were obtained from the traps on Clear and Cub creeks. Tagged fish were generally removed from the traps in the afternoon but some were removed at other times of the day. The tag number, date, time of day, length and sex of each recaptured fish were recorded. A few tagged fish were taken by anglers. The heads of all recaptured anosmic fish were saved and the olfactory chambers examined to see if the plugs were intact.

Release points 2 and 3 were used for tracking experiments. Fish moving upstream to spawn were obtained from the traps on Clear, Cub, and Pelican creeks, with a dip net from Hatchery Creek (3.6 km west of Pelican Creek), and by hook and line from Arnica Creek. Non-spawning fish were caught with hook and line 8.4 km west-northwest (point A) and 10.1 km west-southwest (point B), respectively, of the mouth of Clear Creek (Fig. 1).

Tracking experiments were conducted from May 31 to July 28, 1966, and June 16 to July 25, 1967. Groups of 2-6 fish were taken to a release point in a covered tub. Four types of experimental fish were used: non-anesthetized, blind, blind-anosmic and control. Treatments for each type were the same as for tagging experiments except that control fish used in comparison with the blind fish were anesthetized only.

A float-tracking device consisting of a 5 cm^3 Styrofoam (Dow Chemical Co.) cube connected by 2 m of nylon line to an alligator clip was attached to the dorsal fin of each fish at a release point (Jahn, 1966). For experiments at point 2, 2 non-anesthetized fish or one blind and one control fish were liberated at one-minute intervals without attempt to orient them. For experiments at point 3, 2-5 non-anesthetized, 2 blind-ansomic and 3 control, or 3 blind-anosmic and 2 control fish were similarly released. After the fish were released a drift drogue was placed in the water to determine currents at the approximate depth the fish were swimming (Jahn, 1966).

Positions of the fish and drift drogue were determined by sighting on landmarks with a sextant. Sightings were taken at $\frac{1}{2}$-hour intervals on each fish and the drogue released at point 2. In a few instances fish were lost for a time. Experiments were terminated either at 2 hours or when experimental fish reached an area where I could see the lake bottom or when windy weather prevented accurate sightings. Only one sighting was taken on each fish and the drogue released at point 3 — either one hour after the experiment began or sooner if the wind interfered with sightings. This terminated an experiment and the fish and drogue were picked up as quickly as possible. Most fish were recovered and the length and sex of each were determined. Most spawning fish were tagged and released, but non-spawning fish were cut open to determine sex. The fish tracked at point 2 included 34 spawning fish from Clear Creek, 26 from Cub Creek and 10 from Pelican Creek, and in addition, 21 non-spawning and 2 spawned-out fish caught at point A. Those tracked from point 3 included 61 spawning fish from Clear Creek, 20 from Cub Creek, 23 from Arnica Creek and 4 from Hatchery Creek, and in addition, 24 non-spawning and 6 spawned-out fish caught at points A and B.

Underwater photographs were taken to determine if landmarks might be visible. A Nikonos All-Weather camera (Ehrenreich Photo-Optical Industries, Inc.) was attached to the end of a pipe 3 m long so the camera faced upward at an angle of 48° from the vertical (toward the edge of the "fish window", Walls, 1942). Light readings for each picture were taken just under the surface of the lake with a Sekonic Model L-86 light meter in a waterproof housing (Ehrenreich Photo-Optical Industries, Inc.). Pictures were taken using black and white Tri-X Pan film (Eastman Kodak Co.) from depths of 0.5, 1.0 and 2.0 m at release points 2 and 3. Some were also taken from 1.0 and 2.0 m, 20-80 m from shore. The shutter was released by a cord attached to a lever while the camera was held in the desired position.

An attempt was made to train hatchery cutthroat trout (150-213 mm total length) in the laboratory to use a light source as a reference point for orientation. The training tank (2 m in dia.) was similar to that used by Hasler et al. (1958) and contained 16 wedge-shaped boxes facing outward from a central release chamber. The light source was above the edge of the tank at an angle of 50° from the center. The tank was completely enclosed by black curtains which blocked out extraneous light and hid the experimenter from the fish. All fish were trained individually at nearly the same time each day for 6 days in succession with one day's intermission. Two fish were subjected to 5 trials per day for 30 consecutive days using a 100-watt light bulb and 6 fish 10 trials per day for 10 consecutive days using a 300-watt bulb. Three fish were trained to go 90° clockwise, 3 90° counterclockwise and 2 toward the light source. Three untrained fish were used as controls.

Each fish to be trained was netted from a trough, placed in the central chamber of the tank and released after it quieted down. During training only one of the 16 boxes was made available for the fish to hide in. An electric probe was used to shock and direct the fish to the open box. After the fish entered the box, it was left undisturbed for one minute and then netted and returned to the central chamber. This process was repeated for the remaining trials. The number of trials used for training was the same as that for testing, but during testing all 16 boxes were available for the fish to hide in. The tank and position of the light were rotated after each day's training to prevent use of marks on the tank and other cues for orientation. In addition the experimenter changed locations to avoid being used as a reference point. Fish were tested the day after the last training session at the normal training time. Those which oriented were retested the following day without additional training 6 hours after their usual training time. Retention of learning was also tested.

Data from tagging and tracking experiments were analyzed with the aid of a computer. Chi-square contingency tables (Steel and Torrie, 1960) were used to compare homing, straying and total recapture of each experimental group with every other for tagging experiments. A mean direction (a), a mean vector length (r) (Batschelet, 1965), average swimming speed and average length of fish were calculated for each experimental group used in tracking experiments. A Rayleigh test (Greenwood and Durand, 1955) was applied to each male, female and combined sex group to determine if the distributions were uniform. A resultant vector F test (Watson and Williams, 1956) was used to compare combined sex groups with each other to see if the mean directions of each pair were significantly different. An R test (Watson and Williams, 1956; Stephens, 1962) was used to determine if the mean direction of each male, female and combined sex group except non-spawning and spawned-out fish was toward the homestream. Current direction and sun azimuth were taken as the zero direction for each fish instead of true North. Mean directions, Rayleigh tests and resultant vector F tests were then recalculated for combined sex groups. Summaries of all these tests are given by Batschelet (1965). The normal approximation test (Steel and Torrie, 1960) was used to determine if experimental fish were trained in the laboratory.

RESULTS

HOMING STUDIES

Fish used in tagging studies were of 2 types: groups taken from the traps as contrasted to individual fish tagged after tracking.

Group Tagging. Two hundred non-anesthetized, 50 anosmic, 50 blind-anosmic, 50 controls for anosmic fish and 25 controls for blind-anosmic fish from Clear Creek and 100 non-anesthetized from Cub Creek were used in group tagging experiments. Forty-one percent of all non-anesthetized fish from Clear Creek homed and 5.5% strayed while 33.0% of non-anesthetized fish from Cub Creek homed and 15.0% strayed (Table I).

Table I. Displacement and recapture of Clear and Cub creek trout during June and July, 1966 and 1967. (Percentages in parentheses.)

Year	Release point	Origin creek	Group[a]	Number released	Number recaptured Home	Stray	Angler	Total
1966	2	Clear	NA	50	20(40.0)	3(6.0)	0	23(46.0)
		Cub	NA	50	21(42.0)	7(14.0)	2(4.0)	30(60.0)
	3	Clear	NA	50	24(48.0)	3(6.0)	2(4.0)	29(58.0)
		Cub	NA	50	12(24.0)	8(16.0)	2(4.0)	22(44.0)
1967	1	Clear	NA	50	15(30.0)	5(10.0)	1(2.0)	21(42.0)
	3	Clear	A	50	6(12.0)	1(2.0)	2(4.0)	9(18.0)
			CA	50	23(46.0)	5(10.0)	2(4.0)	30(60.0)
			BA	50	2(4.0)	0	0	2(4.0)
			CBA	25	10(40.0)	0	0	10(40.0)
	4	Clear	NA	50	23(46.0)	4(8.0)	1(2.0)	28(56.0)

[a] NA - non-anesthetized; A - anosmic; BA - blind-anosmic; CA - control anosmic; CBA - control blind-anosmic.

Twelve percent of anosmic fish from Clear Creek homed and 2.0% strayed while 46.0% of control fish homed and 10.0% strayed. Only 2.0% of blind-anosmic fish from Clear Creek homed while 40.0% of control fish homed.

Significantly fewer anosmic and blind-anosmic fish from Clear Creek homed and strayed than other experimental groups (Tables II, III, IV). Significantly fewer non-anesthetized fish from Cub Creek released at point 3 homed than non-anesthetized fish from Clear Creek released at points 3 or 4.

Average homing times were less for non-anesthetized fish from Clear Creek released at point 1 than for any other group (Table V). Non-anesthetized fish from Clear Creek homed faster on the average from point 4 (22.0 km) in 1967 than from points 2 or 3 (0.5 and 5.0 km, respectively) in 1966. Non-anesthetized fish from Clear and Cub creeks homed in about the same length of time. The average homing time of anosmic fish from Clear Creek was greater than any other experimental group, and 63 hours greater than control fish. Blind-anosmic fish from Clear Creek homed as quickly as control fish. Statistical analyses are not given for homing times since recaptures were not obtained randomly.

Tagging After Tracking. Thirty-seven non-anesthetized, 17 blind-anosmic, 8 blind, 10 controls for blind-anosmic fish and 8 controls for blind fish from Clear Creek, 29 non-anesthetized, 6 blind and 6 controls from Cub Creek, and 10 non-anesthetized fish from Pelican Creek were used to determine homing performance after tracking. Homing percentages of

Table II. Significantly different comparisons of total recapture calculated from Chi-square contingency tables.

Year	Release point	Origin creek	Group[a]	vs.	Year	Release point	Origin creek	Group[a]	Chi-square[b]
1967	3	Clear	A		1966	2	Clear	NA	13.42**
							Cub	NA	20.06**
						3	Clear	NA	18.25**
							Cub	NA	9.89*
					1967	1	Clear	NA	8.91*
						3	Clear	CA	19.86**
								CBA	8.70*
						4	Clear	NA	17.82**
1967	3	Clear	BA		1966	2	Cub	NA	36.22**
						3	Clear	NA	34.18**
							Cub	NA	22.40**
					1967	1	Clear	NA	20.62**
						3	Clear	CA	36.16**
						4	Clear	NA	32.29**

a/ Legend as in Table I.

b/ *Significant at P = 0.05; **Significant at P = 0.01.

Table III. Significantly different comparisons of homing calculated from Chi-square contingency tables.

Year	Release point	Origin creek	Group[a]	vs.	Year	Release point	Origin creek	Group[a]	Chi-square[b]
1966	3	Cub	NA		1966	3	Clear	NA	4.72*
					1967	3	Clear	CA	4.68*
						4	Clear	NA	3.89*
1967	3	Clear	A		1966	2	Clear	NA	10.42**
							Cub	NA	15.22**
						3	Clear	NA	17.21**
							Cub	NA	3.91*
					1967	1	Clear	NA	5.82*
						3	Clear	CA	17.05**
								CBA	7.00*
						4	Clear	NA	15.65**
1967	3	Clear	BA		1966	2	Clear	NA	20.53**
							Cub	NA	26.59**
						3	Clear	NA	28.99**
							Cub	NA	11.43**
					1967	1	Clear	NA	14.30**
						3	Clear	CBA	16.07**
								CA	28.80**
						4	Clear	NA	27.10**

a/ Legend as in Table I.

b/ *Significant at P = 0.05; **Significant at P = 0.01.

Table IV. Significantly different comparisons of straying calculated from Chi-square contingency tables.

Year	Release point	Origin creek	Group[a]	vs.	Year	Release point	Origin creek	Group[a]	Chi-square[b]
1966	3	Cub	NA		1967	3	Clear	CBA	3.95*
1967	3	Clear	A		1966	2	Cub	NA	7.47*
						3	Cub	NA	8.88*
					1967	1	Clear	NA	3.92*
						3	Clear	CA	5.96*
						4	Clear	NA	3.98*
1967	3	Clear	BA		1966	2	Clear	NA	4.99*
							Cub	NA	13.72**
						3	Clear	NA	6.26*
							Cub	NA	11.78**
					1967	1	Clear	NA	7.51*
						3	Clear	CA	10.30**
						4	Clear	NA	7.80**

a/ Legend as in Table I.

b/ *Significant at P = 0.05; **Significant at P = 0.01.

Table V. Time (hrs) from release to recapture of Clear and Cub creek trout released during June and July, 1966 and 1967.

Year	Release point	Origin creek	Group[a]	Number released	Home No.	Home Range	Home Av.	Stray No.	Stray Range	Stray Av.
1966	2	Clear	NA	50	20	8-201	109	3	26-223	94
		Cub	NA	50	20[b]	71-226	117	7	8-100	74
	3	Clear	NA	50	24	34-392	148	3	32-250	135
		Cub	NA	50	12	35-221	131	8	29-249	105
1967	1	Clear	NA	50	15	6-142	60	5	19- 94	39
	3	Clear	A	50	6	121-219	160	1	113	113
			CA	50	23	22-293	97	5	48-360	165
			BA	50	2[c]	96-120	108	0	0	0
			CBA	25	10	50-312	113	0	0	0
	4	Clear	NA	50	23	45-216	90	4	45- 96	61

[a] Legend as in Table I.

[b] Does not include one fish whose tag was found in the bottom of the Cub Creek trap 434 hours after release.

[c] Seen in stream, and not caught in the trap.

these experimental groups of fish (Table VI) were similar to those used in group tagging experiments, except only one of 10 controls for blind-anosmic fish homed after tracking.

Significantly fewer blind-anosmic fish from Clear Creek homed than all other groups tagged after tracking except non-anesthetized fish from Cub Creek (released at point 3) and controls for blind-anosmic fish (Table VII). Blind and control fish from Cub Creek tracked from point 2 homed equally well. No fish from Pelican or Arnica creeks were found among the

Table VI. Recapture of Clear and Cub creek trout tagged and released after tracking experiments in 1966 and 1967. (Percentages in parentheses.)

Year	Release point	Origin creek	Group[a]	Number released	Number recaptured: Home	Stray	Angler	Total
1966	2	Clear	NA	18	6(33.3)	1(5.5)	0	7(38.8)
			B	8	4(50.0)	0	0	4(50.0)
			CB	8	5(62.5)	0	0	5(62.5)
		Cub	NA	14	7(50.0)	0	0	7(50.0)
			B	6	5(83.5)	0	0	5(83.5)
			CB	6	3(50.0)	0	0	3(50.0)
		Pelican	NA	10	0	0	0	0
	3	Clear	NA	14	6(42.8)	0	0	6(42.8)
		Cub	NA	15	3(20.0)	5(33.3)	0	8(53.3)
1967[b]	3	Clear	NA	5	4(80.0)	0	0	4(80.0)
			BA	17	1(5.9)	0	1(5.9)	2(11.8)
			CBA	10	1(10.0)	2(20.0)	1(10.0)	4(40.0)

a/ NA — non-anesthetized; B — blind; CB — control blind; BA — blind-anosmic; CBA — control blind-anosmic.

b/ Only those released after the fish traps were permanently installed are considered. Fish from Arnica Creek are not included since there was no trap operated there.

Table VII. Significantly different comparisons of total recapture, homing, and straying of trout tagged and released after tracking, calculated from Chi-square contingency tables.[c]

Year	Release point	Origin creek	Group[a]	vs.	Year	Release point	Origin creek	Group[a]	Chi-square[b]
				Total Recapture					
1966	2	Cub	B		1967	3	Clear	CBA	8.78*
	3	Cub	NA			3	Clear	BA	9.10*
				Homing					
1966	2	Pelican	NA		1966	2	Clear	NA	4.53*
								B	6.42*
								CB	8.65**
							Cub	NA	7.05**
								B	12.12**
								CB	6.15*
						3	Clear	NA	5.71*
					1967	3	Clear	NA	10.90**
		Cub	B		1966	2	Clear	NA	4.10*
						3	Cub	NA	4.26*
					1967	3	Clear	CBA	6.19*
1967	3	Clear	BA		1966	2	Clear	NA	4.16*
								B	6.18*
								CB	9.00**
							Cub	NA	7.30**
								B	13.07**
								CB	5.61*
						3	Clear	NA	5.59*
					1967	3	Clear	NA	11.42**
1967	3	Clear	NA		1967	3	Clear	CBA	5.18*
				Straying					
1966	3	Cub	NA		1966	2	Cub	NA	3.95*
							Pelican	NA	5.39*
1967	3	Clear	BA		1966	3	Cub	NA	7.02**
					1967	3	Clear	CBA	4.10*

a/ Legend as in Table VI.

b/ *Significant at P = 0.05; **Significant at P = 0.01.

c/ Fish from Arnica Creek were not included since there was no trap operated there.

recaptures.

The average homing times for blind fish from Clear and Cub creeks were 78 and 146 hours greater, respectively, than for control fish (Table VIII).

Table VIII. Time (hrs) from release to recapture of trout tagged after tracking experiments, 1966 and 1967.

Year	Release point	Origin creek	Group[a]	Number released	Home No.	Home Range	Home Av.	Stray No.	Stray Range	Stray Av.
1966	2	Clear	NA	18	6	29-462	177	1	297	297
			B	8	4	167-392	263	0	0	0
			CB	8	5	5-339	185	0	0	0
		Cub	NA	14	7	48-340	180	0	0	0
			B	6	5	102-413	302	0	0	0
			CB	6	3	29-340	156	0	0	0
	3	Clear	NA	14	6	104-272	197	0	0	0
		Cub	NA	15	3	199-247	215	5	56-103	87
1967	3	Clear	NA	5	4	36-159	99	0	0	0
			BA	17	1	339	339	0	0	0
			CBA	10	1	241	241	2	69-214	142

[a] Legend as in Table VI.

Control and non-anesthetized fish from Clear and Cub creeks homed in about the same time from point 2 in 1966. The average homing times of non-anesthetized fish from Clear and Cub creeks (tagged after tracking in 1966) from point 2 were 20 and 35 hours less, respectively, than those tagged after tracking from point 3.

The average homing times of non-anesthetized fish from Clear and Cub creeks (1966) tagged after tracking from point 2 were 68 and 63 hours greater, respectively, than similarly treated fish used in group tagging experiments. The average homing times of non-anesthetized fish from Clear and Cub creeks (1966) tagged after tracking from point 3 were 39 and 84 hours greater, respectively, than similarly treated fish used in group tagging experiments.

FLOAT-TRACKING STUDIES

Experiments from Point 2. A total of 94 fish was tracked from point 2. The experimental groups and directions of orientation were as follows: non-anesthetized fish from Clear Creek — east-northeast; controls for blind fish from Clear and Cub creeks — east; non-anesthetized fish from Pelican and Cub creeks and spawned-out fish from point A — east-southeast; blind fish from Clear Creek and non-spawning fish from point A — southeast; and blind fish from Cub Creek — south (Table IX).

Vector lengths (r) were significantly greater than zero for non-anesthetized fish from Clear Creek and non-spawning fish from point A. Non-significant r values for other fish may be due to small sample size rather than lack of orientation. R values and average swimming speeds often decreased after the first $\frac{1}{2}$-hour interval sighting was made. Blind fish had smaller r values than either the control or non-anesthetized fish. Non-spawning fish oriented as well as or better than any other experimental group of fish.

Mean directions of all groups of spawning fish at the conclusion of all tracking experiments were not significantly different from the home-stream direction, except for non-anesthetized fish from Pelican and Clear

Table IX. Mean directions (from true North), vector lengths, swimming speeds, Rayleigh tests and homestream tests at $\frac{1}{2}$-hr intervals for fish tracked from point 2 (1966).

Origin creek	Group[d/]	Number tracked	Hr after release	Mean direction	Vector length	Speeds (m/hr) Range	Average	Rayleigh test[a/]	Homestream test[a/]
Pelican	NA	9	0.5	125°	0.7797	97-779	434	5.47**	7.02**
		3	1.0	223	0.3730	83-151	111	-[b]	-[b]
		4	1.5	188	0.1575	71-291	139	-[b]	0.63
		3	2.0	293	0.3620	79-199	158	-[b]	-[b]
		10	Term.	114	0.5057	79-779	408	2.55	5.06*
Clear	NA	16	0.5	83	0.3926	20-622	325	2.47	6.28
		14	1.0	58	0.2971	82-519	294	1.24	4.16
		10	1.5	20	0.5509	80-512	213	3.04*	5.51*
		7	2.0	16	0.8651	45-508	171	5.24**	6.06**
		18	Term.	68	0.5445	45-622	323	5.34**	9.80**
Clear	B	8	0.5	137	0.2995	178-968	481	0.72	2.40
		6	1.0	78	0.2863	156-674	345	0.49	1.72
		3	1.5	48	0.5900	131-317	231	-[b]	-[b]
		2	2.0	27	0.4383	120-289	205	-[b]	-[b]
		8	Term.	130	0.3669	120-968	502	1.08	2.94
Clear	CB	8	0.5	69	0.6430	259-977	556	3.31*	5.14*
		5	1.0	32	0.3747	106-558	350	-[b]	1.87
		3	1.5	98	0.1692	129-225	190	-[b]	-[b]
		1	2.0	330	1.0000	189	189	-[b]	-[b]
		8	Term.	94	0.4146	189-977	503	1.38	3.31
Cub	NA	14	0.5	228	0.1781	125-760	367	0.44	2.49
		11	1.0	248	0.2620	36-473	243	0.76	2.88
		8	1.5	319	0.0082	134-272	214	0.00	0.66
		5	2.0	31	0.1792	86-255	181	-[b]	0.90
		14	Term.	121	0.2730	86-760	336	1.04	3.82

Table IX. Continued.

Origin creek	Group[d]	Number tracked	Hr after release	Mean direction	Vector length	Speeds (m/hr) Range	Average	Rayleigh test[a]	Homestream test[a]
Cub	B	6	0.5	109°	0.3162	132-569	314	0.60	1.89
		5	1.0	113	0.3623	182-407	272	-[b]	1.81
		4	1.5	57	0.5494	147-484	259	-[b]	2.19
		3	2.0	199	0.2742	124-183	162	-[b]	-[b]
		6	Term.	175	0.2057	124-484	285	0.25	1.23
Cub	CB	6	0.5	99	0.5488	332-966	576	1.80	3.29**
		3	1.0	99	0.7290	217-445	344	-[b]	-[b]
		1	1.5	61	1.0000	168	168	-[b]	-[b]
		1	2.0	57	1.0000	143	143	-[b]	-[b]
		6	Term.	98	0.4666	143-966	509	1.30	2.8C
—	NS	22	0.5	133	0.5445	331-962	592	6.52**	-[c]
		7	1.0	181	0.5650	357-650	514	2.23	-[c]
		1	1.5	285	1.0000	419	419	-[b]	-[c]
		1	2.0	301	1.0000	251	251	-[b]	-[c]
		22	Term.	131	0.5849	251-962	586	7.52**	-[c]
—	SO	2	0.5	104	0.8191	533-736	634	-[b]	-[c]
		2	Term.	104	0.8191	533-736	634	-[b]	-[c]

a/ *Significant at P = 0.05; **Significant at P = 0.01.

b/ Sample too small for test.

c/ Does not apply.

d/ NS — non-spawning; SO — spawned-out; NA — non-anesthetized; B — blind; CB — controls for blind.

creeks. The mean directions of all groups of fish were not significantly different from each other, except that those of non-anesthetized fish from Clear Creek and non-spawning fish differed significantly. However, when either the sun azimuth or the current direction was used as the zero direction instead of true North, the mean directions of these latter groups were not significantly different (Tables X, XI). The average speed, mean direction, and vector length for currents were 165 m/hr, 158° and 0.8076, respectively.

Non-spawning and spawned-out fish had the fastest average swimming speeds of all groups tested (586 and 634 m/hr, respectively). Average swimming speeds for non-anesthetized, blind and control fish from Clear Creek were 323, 502 and 503 m/hr, respectively, and from Cub Creek 336, 285 and 509 m/hr, respectively. Non-anesthetized fish from Pelican Creek averaged 408 m/hr.

The mean directions of males and females were not significantly different, except for blind fish from Cub Creek. Females did not have consistently greater vector lengths than males (Table XII), but they generally had greater average swimming speeds.

Experiments from Point 3. The total numbers of fish tracked from point 3 in 1966 and 1967 were 59 and 79, respectively. The experimental groups and directions of orientation for fish tracked in 1966 were as follows: non-anesthetized fish from Clear and Cub creeks and non-spawning fish from points A and B — east-northeast; and spawned-out fish from points

Table X. Mean directions and vector lengths at termination of tracking experiments from points 2 and 3, 1966 and 1967, using true North, sun azimuth, and current direction as the zero directions.

				Zero direction as					
				True North		Sun azimuth		Current	
Year	Origin creek	Group[a]	No.	Mean direction	Vector length	Mean direction	Vector length	Mean direction	Vector length
				POINT 2					
1966	Pelican	NA	10	114°	0.5057	24°	0.5027	65°	0.2421
	Clear	NA	18	68	0.5445	319	0.3746	297	0.2236
		B	8	130	0.3669	359	0.3677	26	0.6392
		CB	8	94	0.4146	330	0.6493	9	0.2085
	Cub	NA	14	121	0.2730	339	0.3751	49	0.1401
		B	6	175	0.2057	315	0.7240	343	0.4335
		CB	6	98	0.4666	323	0.6041	329	0.8243
	—	NS	22	131	0.5849	358	0.7147	303	0.2377
	—	SO	2	104	0.8191	323	0.8743	258	0.5446
				POINT 3					
1966	Clear	NA	14	63	0.5079	313	0.4992	341	0.3242
	Cub	NA	15	71	0.4156	288	0.4555	30	0.3623
	—	NS	24	75	0.6465	308	0.5217	117	0.5911
	—	SO	6	123	0.4881	313	0.3278	114	0.4237
1967	Clear	NALA	13	302	0.9235	3	0.9122	5	0.8708
		BA	20	11	0.5130	240	0.4926	32	0.6045
		CBA	14	59	0.3162	296	0.2501	53	0.5212
	Arnica	NA	23	119	0.2679	335	0.3018	18	0.4608
	Cub	NA	5	96	0.6561	257	0.7315	166	0.5393
	Hatchery	NA	4	199	0.5049	82	0.5389	304	0.5049

[a] NALA — non-anesthetized tracked late in the afternoon; BA — blind-anosmic; CBA — controls for blind-anosmic. Others given in legend for Table IX.

Table XI. Comparisons of direction test (F) values using true North, sun azimuth, and current direction as zero directions.

Year	Origin creek	Group[b]	vs.	Year	Origin creek	Group[b]	Direction test (F) value[a] with zero direction as North	Azimuth	Current
					POINT 2				
1966	Clear	NA		1966	—	NS	7.05*	2.27*	0.01
					POINT 3				
1967	Clear	NALA		1966	—	NS	58.86**	7.78**	9.53**
					—	SO	24.50**	2.05	10.25**
					Clear	NA	27.74**	5.20*	0.65
					Cub	NA	23.33**	9.96**	0.82
				1967	Clear	BA	11.11**	31.10**	2.00
						CBA	13.32**	3.79	4.61
					Arnica	NA	23.47**	1.09	0.34
					Hatchery	NA	11.74**	7.79*	3.78
					Cub	NA	35.95**	26.74**	20.89**
1967	Hatchery	NA		1966	—	NS	7.60*	6.93*	6.35*
					Clear	NA	5.94*	5.93*	0.40
					Cub	NA	4.77*	9.42*	2.27
				1967	Clear	BA	7.54*	7.53*	3.94
						CBA	4.56*	4.62*	4.47
1967	Clear	BA		1966	—	NS	8.53**	7.35*	2.29
					—	SO	6.78*	2.09	0.15
				1967	Arnica	NA	9.61**	8.19**	0.32
					Cub	NA	4.99*	0.24	9.92**

a/ *Significant at P = 0.05; **Significant at P = 0.01.

b/ Legend as for Table X.

Table XII. Mean directions (from true North), vector lengths, swimming speeds, Rayleigh tests, homestream tests and direction tests (F) for males and females at termination of tracking experiments from point 2 (1966).

Origin creek	Group[d]	Sex	Number tracked	Mean direction	Vector length	Speeds (m/hr) Range	Speeds (m/hr) Average	Rayleigh test[a]	Homestream test[a]	Direction test[a]
Pelican	NA	♂	2	230°	0.1132	79-199	139	-[b]	-[b]	0.57
		♀	8	112	0.6448	196-779	475	3.32*	5.16**	
Clear	NA	♂	5	9	0.4988	45-351	162	-[b]	2.49	3.51
		♀	13	82	0.6757	110-622	386	5.94**	8.79**	
Clear	B	♂	3	106	0.7271	120-968	468	-[b]	-[b]	0.68
		♀	5	173	0.2542	177-843	523	-[b]	1.27	
Clear	CB	♂	2	74	0.9612	214-537	376	-[b]	-[b]	0.35
		♀	6	118	0.2751	189-977	546	0.45	1.65	
Cub	NA	♂	8	162	0.4873	159-760	389	1.90	3.89**	4.54
		♀	6	50	0.4531	86-568	265	1.23	2.71	
Cub	B	♂	3	166	0.8486	124-402	237	-[b]	-[b]	4.98*
		♀	3	339	0.4440	177-484	334	-[b]	-[b]	
Cub	CB	♂	4	93	0.3112	143-688	429	-[b]	1.24	0.01
		♀	2	103	0.7826	371-966	668	-[b]	-[b]	
—	NS	♂	10	118	0.4386	251-815	608	1.92	-[c]	0.34
		♀	12	137	0.7195	357-962	567	6.21**	-[c]	
—	SO	♂	1	139	1.0000	533	533	-[b]	-[b]	0.00
		♀	1	69	1.0000	736	736	-[b]	-[b]	

a/ *Significant at P = 0.05; **Significant at P = 0.01.

b/ Sample too small for test.

c/ Does not apply.

d/ Legend as for Table IX.

A and B — east-southeast. Those observed for fish tracked in 1967 were as follows: blind-anosmic fish from Clear Creek — north; controls for blind-anosmic fish from Clear Creek — east-northeast; non-anesthetized fish from Cub Creek — east; non-anesthetized fish from Arnica Creek — east-southeast; non-anesthetized fish from Hatchery Creek — south-southwest; non-anesthetized fish from Clear Creek tracked in the late afternoon — west-northwest (Table XIII).

Vector lengths (r) were significantly greater than zero for non-anesthetized and blind-anosmic fish from Clear Creek and non-spawning fish from points A and B. Non-anesthetized fish from this creek tracked from point 3 during the late afternoon oriented the best of all experimental groups.

Non-anesthetized fish tracked in the late afternoon and blind-anosmic fish from Clear Creek and non-anesthetized fish from Arnica Creek were the only groups whose mean directions differed significantly from the home-stream direction. The mean direction of non-anesthetized fish from Clear Creek tracked in the late afternoon differed significantly from the mean directions of all other groups (Table XI). These differences became non-significant when either the sun azimuth or current direction was used as the zero direction instead of true North. However, non-spawning fish and non-anesthetized fish from Cub Creek (1967) differed significantly from non-anesthetized fish from Clear Creek tracked in late afternoon. Eight of 9 significant differences between mean directions of other groups of fish became non-significant when similarly treated (Table XI). The

Table XIII. Mean directions (from true North), vector lengths, swimming speeds, Rayleigh tests and homestream tests at termination of tracking experiments from point 3, 1966 and 1967.

Year	Origin creek	Group[d]	Number tracked	Mean direction	Vector length	Speeds (m/hr) Range	Speeds (m/hr) Average	Rayleigh test[a]	Homestream test[a]
1966	Clear	NA	14	63°	0.5079	98- 787	396	3.61*	7.11
	Cub	NA	15	71	0.4156	118- 901	374	2.59	6.23
	—	NS	24	75	0.6465	85-1484	545	10.03**	-[c]
	—	SO	6	123	0.4881	162- 692	458	1.43	-[c]
1967	Clear	NALA	13	302	0.9235	136- 959	562	11.08**	12.00**
		BA	20	11	0.5130	33- 718	353	5.26*	10.26**
		CBA	14	59	0.3162	213- 639	360	1.40	4.43
	Arnica	NA	23	119	0.2679	48- 670	349	1.65	6.16**
	Cub	NA	5	96	0.6561	185- 473	347	-[b]	3.28
	Hatchery	NA	4	199	0.5049	26- 413	219	-[b]	2.01

a/ *Significant at P = 0.05; **Significant at P = 0.01.

b/ Sample too small for test.

c/ Does not apply.

d/ NA — non-anesthetized; NS — non-spawning; SO — spawned-out; NALA — non-anesthetized late afternoon; BA — blind-anosmic; CBA — controls for blind-anosmic.

average speed, mean direction and vector length for currents in 1966 were 402 m/hr, 25°, and 0.6867 respectively, and in 1967 were 398 m/hr, 319°, and 0.5464, respectively.

Non-spawning and non-anesthetized fish from Clear Creek tracked in the late afternoon had the fastest average swimming speeds of all groups tested (545 and 562 m/hr, respectively). In 1966 average swimming speeds in m/hr for other groups were 396 and 374 for non-anesthetized fish from Clear and Cub creeks, respectively, and 458 for spawned-out fish. In 1967 they were 349, 347 and 219 for non-anesthetized fish from Arnica, Cub and Hatchery creeks, respectively, and 353 and 360 for blind-anosmic and control fish from Clear Creek, respectively.

The mean directions of males and females were not significantly different, except for the blind-anosmic controls from Clear Creek. Males did not consistently have greater vector lengths than females (Table XIV). However, males generally had greater average swimming speeds than females released from point 3.

UNDERWATER PHOTOGRAPHS

Underwater photographs were taken to see if the images of shoreline features could be recorded photographically at the approximate depths which the fish swam when tracked from points 2 and 3. No land features were visible on pictures taken from depths of 0.5, 1.0 and 2.0 m at points 2 and 3. Clouds were visible on several of these pictures. Tops of trees were distinguishable on a few pictures taken from depths of 1.0 and 2.0 m

Table XIV. Mean directions (from true North), vector lengths, swimming speeds, Rayleigh tests, homestream tests and direction tests (F) for males and females at termination of tracking experiments from point 3, 1966 and 1967.

Year	Origin creek	Group[d]	Sex	Number tracked	Mean direction	Vector length	Speeds (m/hr) Range	Speeds (m/hr) Average	Rayleigh test[a]	Homestream test[a]	Direction test[a]
1966	Clear	NA	♂	6	114°	0.1954	161- 766	335	0.22	1.17	1.23
			♀	7	46	0.8722	99- 787	459	5.32**	6.11*	
	Cub	NA	♂	8	87	0.8124	118- 901	397	5.28**	6.49	4.02
			♀	7	341	0.2582	142- 518	347	0.46	1.81	
	—	NS	♂	15	84	0.7926	85-1484	586	9.42*	-[c]	2.04
			♀	8	51	0.6491	168- 782	497	3.37*	-[c]	
	—	SO	♂	1	69	1.0000	692	692	-[b]	-[c]	0.86
			♀	5	142	0.4946	162- 670	411	-[b]	-[c]	
1967	Clear	NALA	♂	1	278	1.0000	277	277	-[b]	-[b]	0.50
			♀	8	246	0.9376	136- 959	573	7.03**	7.50**	
		BA	♂	6	5	0.4607	118- 718	381	1.27	2.76	0.05
			♀	13	14	0.5021	33- 713	352	3.27*	6.52*	
		CBA	♂	2	266	0.9925	251- 357	304	-[b]	-[b]	13.71**
			♀	10	62	0.7293	213- 639	394	5.31*	7.29*	
	Arnica	NA	♂	13	104	0.2730	123- 670	388	0.96	3.54**	0.77
			♀	9	149	0.4094	48- 670	287	1.50	3.68**	
	Cub	NA	♂	4	81	0.6532	185- 473	330	-[b]	2.61	0.71
			♀	1	137	1.0000	415	415	-[b]	-[b]	
	Hatchery	NA	♂	1	154	1.0000	287	287	-[b]	-[b]	0.62
			♀	3	227	0.4960	26- 413	197	-[b]	-[b]	

a/ *Significant at P = 0.05; **Significant at P = 0.01.

b/ Sample too small for test.

c/ Does not apply.

d/ Legend as for Table XIII.

(20-80 m from shore). Clouds and trees were only visible on pictures taken when the lake surface was very calm. Even though these images appeared on some photographs, I had no way of knowing whether or not the fish used them for orientation.

TRAINING EXPERIMENTS

An attempt was made to train fish to use a light source as a reference point for orientation. Two fish subjected to 5 trials per day for 30 consecutive days using a 100-w light bulb were not trained at the end of this time (Fig. 2). Three of 6 fish subjected to 10 trials per day for 10 consecutive days using a 300-w light bulb were trained. Two of these tested 6 hours after their normal training time showed no compensation in direction for the change in time. Three untrained fish used as controls generally swam away from the light source. Retention of learning was shown by one fish tested 3 weeks after the last training session.

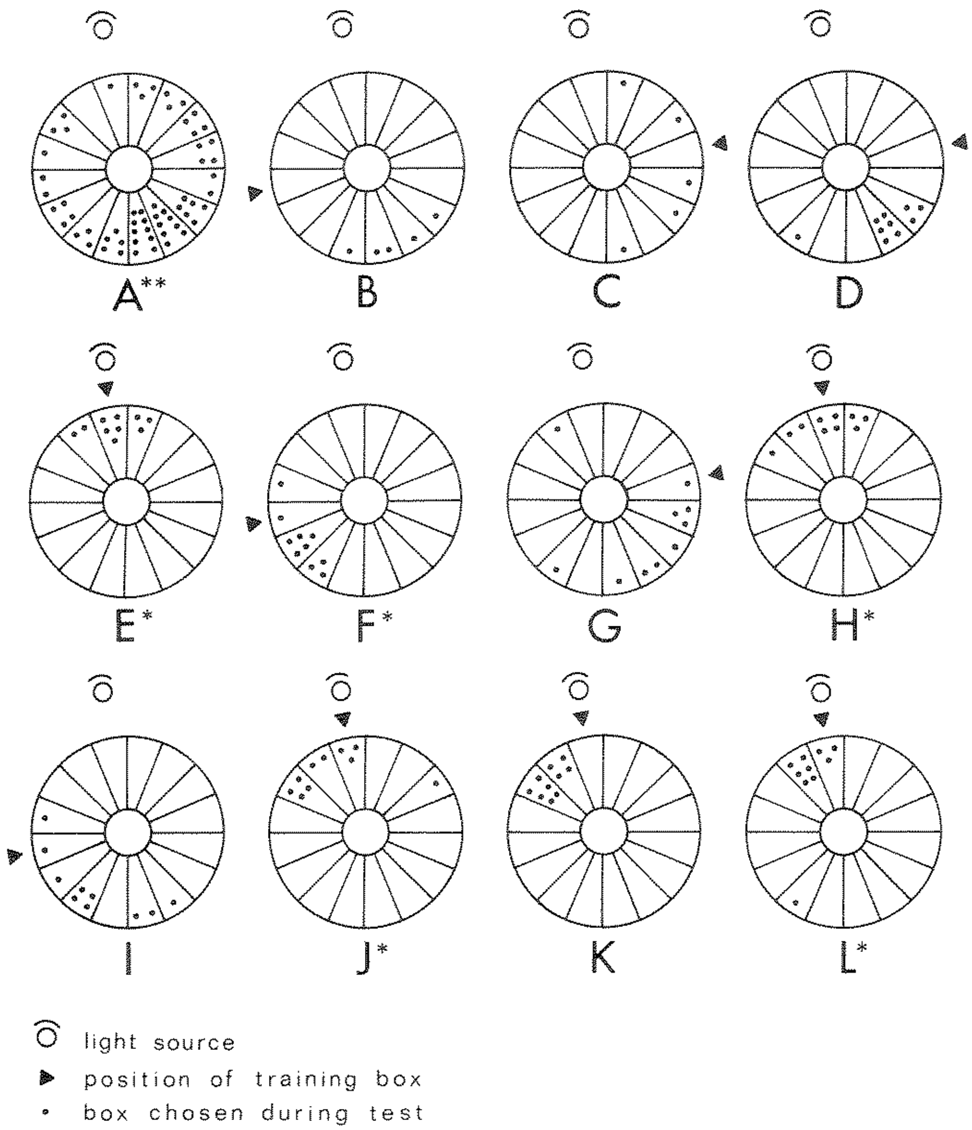

Fig. 2. Results of training experiments using a light source as a reference point for orientation. A — untrained controls; B,C — fish subjected to 5 trials per day, after 30 days training; D,E,F,G,H, I — fish subjected to 10 trials per day, after 10 days training; J,K — fish tested 6 hrs after normal training time (E and H, respectively); L — fish H tested 3 weeks after the last training; * — significant value for normal approximation test at $P = 0.05$; ** — significant value for Chi-square test at $P = 0.01$.

DISCUSSION

Significantly fewer anosmic and blind-anosmic fish homed than other groups. This could be due to the lack of olfaction or vision and olfaction, respectively, or to handling and the trauma of injection of material into the olfactory capsules and eyes. Only 6 of 50 anosmic and 2 of 50 blind-anosmic fish homed after they were displaced 5.0 km. McCleave (1967) found that 7 of 50 anosmic and 25 of 50 blind fish homed. Thus the combination of olfaction and vision together rather than alone seem important to homing. Olfaction was probably more important as the fish neared the homestream but not important in open water (Hasler, 1966; Brett and Groot, 1963). No difference was noted in the percentage of homing for anesthetized (control) and non-anesthetized fish. This was also found by McCleave (ibid.). Handling during anesthetization and the anesthetic did not affect homing ability. Black and Connor (1964) found that anesthetization of rainbow trout did not change blood lactate of muscle glycogen, but Black and Barrett (1957) found that even minimal handling and transportation over a 2-hr period caused increases in muscular activity and blood lactate in cutthroat and steelhead trout.

Ricker (manuscript) suggested that some straying may be an artifact due to "proving", in which a fish may ascend a "wrong" tributary some distance and then reject it. If the fish is caught in a trap on the "wrong" tributary it is recorded as a stray. "Proving" could occur on Clear and Cub creeks since nearly all average straying times were less than homing times. This was also true for the 1966 data given by

McCleave (ibid.). The fact that more Cub Creek than Clear Creek fish strayed might be due to the trap being closer to the lake on Clear Creek (75 m) than on Cub Creek (150 m). If "proving" did occur a short distance upstream from the mouths of the creeks, then higher straying by Cub Creek fish would be expected. Furthermore, when fish were caught in the traps, they were assumed to be in the homestream. This may have been an incorrect assumption.

Average homing times were not always directly related to the distance fish were displaced. Those released just outside the stream mouth had the shortest average homing time, but the average homing time for fish displaced 22.0 km from the homestream was shorter than for those displaced 5.0 km away. It is possible that those fish displaced farthest from the homestream had more opportunity to correct "mistakes" in orientation along the return route, thus arriving in a shorter time. McCleave (ibid.) found an inverse relationship of homing time with distance for fish released in 1966, those being displaced farthest homed fastest. He suggested that displacement may cause physiological and behavioral changes resulting in delay while the trout begins a new sequence of events leading to migration and spawning. The delay could occur near the stream mouth where salmonids are known to congregate before moving upstream. Cope (1956) noted that periodic freshets of cold water cause interruptions in upstream migration of cutthroat trout.

Although homing percentages were similar for fish used in group tagging experiments and after tracking, the latter had greater homing times. Perhaps the fish may have become fatigued after towing the floats.

R values and average swimming speeds often decreased after the first ½-hr sighting was taken for fish tracked from point 2. This might be due to the fish having a shoreward orientation immediately after release, resulting in termination of the experiment in a short time. Fish swimming after the first sighting may have tired towing the float. Average swimming speeds were comparable to those reported by Jahn (1966) and McCleave (ibid.).

Non-spawning fish went the same general direction and had greater r values than other groups of fish. Perhaps these fish were "lost" and followed the sun azimuth, since after correction for sun azimuth the mean angles went from 131° to 358°, and 75° to 308° for those tracked from points 2 and 3, respectively. Spawning and non-spawning white bass tracked in Lake Mendota showed a strong orientation toward the northern spawning ground (Hasler et al., 1965; Gardella, MS, 1967).

Mean directions of most groups of fish were not significantly different from the homestream direction. The same was true for fish tracked by Jahn (1966). This was probably due to the locations of the release points. By swimming toward the sun they were also heading toward their homestreams. Fish tracked by McCleave (1967) had similar mean directions to those of this study and to those of Jahn (ibid.) but were significantly different from the homestream direction. The release points used by McCleave were located in the northern portion of the lake. He suggested that cutthroat trout have the ability to maintain a constant compass direction in the sense of dead reckoning (Type II orientation) rather than the ability to find home by true navigation involving corrective feedback (Type III orientation).

The influence of the sun on orientation was shown by fish from Clear Creek (located on the east side of the lake) that went west-northwest when tracked in the late afternoon and by those from Arnica Creek (located on the west side of the lake) that went east-southeast when tracked in the morning. The mean directions of many groups of fish were closer to 0° and vector length values increased when the zero direction was taken at the sun azimuth. The same was true when current was used as the zero direction. The sun was found important to orientation of cutthroat trout tracked by Jahn (1966) and McCleave (1967). Hasler et al. (1958) found that white bass were disoriented under overcast skies. Winn et al. (1964) showed that the sun was important to orientation of parrot fishes, and Groot (1965) found the sun and polarization pattern of the sky to be important in orientation of sockeye salmon.

Due to the small number of training experiments that were conducted, no relationship could be established with the field data concerning orientation.

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