HOMING AND ORIENTATION OF CUTTHROAT TROUT (SALMO CLARKI) IN YELLOWSTONE LAKE, WITH SPECIAL REFERENCE TO OLFACTION AND VISION

by

JAMES DAVID McCLEAVE

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Zoology

Approved:

____
Head, Major Department

____
Chairman, Examining Committee

____
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

March, 1967

Vita

The writer was born in Atchison, Kansas, 17 December 1939, to Dr. and Mrs. D. Harold McCleave. He resided in Pullman, Washington; Tulsa, Oklahoma; Emporia, Kansas; Great Falls, Montana; and Spearfish, South Dakota. He was graduated from Spearfish High School in 1957. He attended Carleton College, Northfield, Minnesota from 1957 to 1961, and was graduated with an A.B. degree in Biology. In September 1961 he entered graduate study at Montana State University, where he was a Graduate Teaching Assistant and a Trainee supported by a Federal Water Pollution Control Administration Training Grant No. 1T1-WP-1. He was graduated with a M.S. in Zoology in June 1963. During 1963-1964 he was Instructor of Zoology at Montana State University, and in 1964 began study toward the doctorate in Zoology there. He was again a Trainee of the Federal Water Pollution Control Administration and later a Graduate Research Assistant on a grant from the National Science Foundation. In December 1962 he married Barbara E. Wilson of Titusville, New Jersey.

Table of Contents

	Page
Abstract	vii
Introduction	1
Methods and Materials	5
Description of Study Area	5
Displacement Studies	7
Float-tracking Studies	10
Statistical Analyses	13
Displacement Studies	13
Float-tracking Studies	14
Results	15
Displacement Studies	15
Float-tracking Studies	33
Angler Returns	46
Discussion	49
Acknowledgements	56
Literature Cited	56

List of Tables

Page

1. Summary of displacement and recapture of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966 16

2. Chi-square comparisons of the recaptures of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966 ... 18

3. Displacement and recapture of trout of known sex from Clear and Cub Creeks, 15-27 July 1964 22

4. Time (hr) from release to recapture of displaced Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966 ... 23

5. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time of Clear and Cub Creek trout from various release points in 1964, 1965, and 1966 24

6. Duncan's new multiple-range comparisons of the mean homing time of Clear and Cub Creek trout from various release points in 1964, 1965, and 1966 25

7. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time between Clear and Cub Creek trout from open-water points in 1964, 1965, and 1966 27

8. Analysis of variance of the mean homing time between 1965 and 1966 Clear and Cub Creek trout displaced to point B 28

9. Time (hr) from release to recapture in the homestream of male and female trout displaced from Clear and Cub Creeks to open-water points during 1965 and 1966 29

10. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time of male and female Clear and Cub Creek trout displaced to open-water points during late June and July, 1965 and 1966 30

11. Results of displacement of blind, anosmic, control, and non-anesthetized trout from Clear Creek to point B, 1966 31

12. Time (hr) from release to recapture in the homestream of blind, anosmic, control, and non-anesthetized Clear Creek trout displaced to point B, 1966 31

Page

13. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing times of blind, anosmic, control, and non-anesthetized trout from Clear Creek displaced to point B, 1966 32

14. Duncan's new multiple-range comparisons of the mean homing times of blind, anosmic, control, and non-anesthetized trout from Clear Creek displaced to point B, 1966 32

15. Tracking times, mean directions (from true North), vector lengths, Rayleigh tests, and homestream tests of blind, anosmic, control, and non-anesthetized trout from Clear, Cub, and Pelican Creeks tracked beginning at point B, 1965 and 1966 34

16. F test comparisons of mean directions of float-tracked trout between various groups within streams, between streams, and between years 39

17. Mean directions, vector lengths, and directions test comparisons of male and female trout float-tracked at point B, 1965 and 1966 42

18. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and current direction (corrected) as the zero direction 43

19. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and sun azimuth (corrected) as the zero direction 45

20. Recapture of Clear, Cub, and Pelican Creek trout tagged and released following float-tracking at point B, 1966 46

21. Comparison of mean directions and vector lengths of Clear Creek trout recaptured in the homestream with those not recaptured following float-tracking at point B, 1966 47

List of Figures

Page

1. Map of northern portion of Yellowstone Lake showing release points and creeks where experimental cutthroat trout were trapped. Inset shows entire lake and principal tributaries 6

2. Directions of "take-off" (plotted in 2° intervals on odd numbered degrees), mean directions, and vector lengths of (A) blind, anosmic, and control Clear Creek trout, and (B) blind, control, and non-anesthetized Cub Creek trout tracked at point B, 10-29 July, 1965 36

3. Directions of "take-off" (plotted in 2° intervals on odd numbered degrees), mean directions, and vector lengths of blind, anosmic, and control (A) Clear Creek trout, (B) Cub Creek trout, and (C) Pelican Creek trout tracked at point B, 2 June-18 July, 1966 37

4. Float-tracks of three Clear Creek trout beginning at point B: 1. Control trout, 31 July 1965, 6 hr 20 min; 2. Blind trout, 1 August 1965, 3 hr 26 min; 3. Non-anesthetized trout, 31 May 1966, 3 hr 56 min 48

ABSTRACT

The movements of mature cutthroat trout (*Salmo clarki*) displaced from spawning tributaries to Yellowstone Lake were studied during late May to early August, 1964, 1965, and 1966, to determine in-season homing performance and the role of olfaction and vision in homing and orientation. Of 1908 trout tagged and displaced from Clear and Cub Creeks to three release points in the lake and to the mouths of the streams, 614 (32.2%) homed, 119 (6.2%) strayed, and 28 (1.5%) were captured by anglers. Recaptures in 1965 and 1966 were higher, and in 1964 lower, than these averages. A greater percentage of Clear Creek trout than Cub Creek trout homed in 1965 and 1966, but a lesser percentage of Clear Creek trout than Cub Creek trout homed in 1964. Only slight differences in homing performance from various release points occurred. Adjusted mean homing times were 16.4 to 111.8 hr in 1964, 45.7 to 105.8 hr in 1965, and 96.0 to 154.7 hr in 1966. An inverse relation between homing times and distance to the release point was apparent only in 1966. Clear and Cub Creek trout homed in about the same length of time. Homing performance and homing times were similar for males and females. The homing performance of blinded, olfactory occluded, control, and non-anesthetized groups of trout were equal, but the length of homing time for blind trout was much longer than that for the other groups. A general east-north-eastward orientation occurred among blind and control trout from Clear Creek in 1965, and among blind, anosmic, and control trout from Clear and Pelican Creeks in 1966, that were float-tracked from an open-water point. Blind, control, and non-anesthetized trout from Cub Creek moved generally northward in 1965, but in 1966 too few Cub Creek trout were tracked to show orientation. Blind and anosmic trout oriented as well as control trout. The directions of orientation were not in the directions of the homestream, and orientation was not at a constant angle to the current directions or the sun azimuths.

INTRODUCTION

Homing and orientation behavior of mature cutthroat trout (*Salmo clarki*) following displacement from spawning tributaries to Yellowstone Lake was studied during late May to early August, 1964, 1965, and 1966. The objectives were to determine in-season homing performance of tagged, displaced trout, and the role of olfaction and vision in orientation and homing.

Gerking (1959) used the term homing in a general sense to mean the return of fish, following migratory, accidental, or experimental displacement, "to a place formerly occupied instead of going to other equally probable places." He defined equally probable places as areas "occupied by other individuals of the same species" (Gerking 1964). In spawning migrations of fishes, three types of homing are recognized: (1) the return of adults to spawn in the same location in which they were hatched, i.e. "reproductive homing" (Lindsey et al. 1959), parent stream, or natal homing; (2) the return of adults to spawn in subsequent breeding seasons at the location of initial spawning, i.e. repeat homing; and (3) the return of adults within the same breeding season to the location of initial choice following displacement, i.e. in-season homing. Horrall (MS 1961) refers to all three as reproductive homing.

Ball (1955) validated the parent stream homing theory for cutthroat trout in Yellowstone Lake. Of 460 fingerlings marked at age I on their downstream migration from Arnica Creek to the lake, 94 (20.4%) returned at ages III or IV as adults. Nearly all of these must have been recruit spawners, since the majority of Arnica Creek fish spawn initially at ages IV and V with a few at ages III or VI (Bulkley 1961), and the survival for more than one spawning is usually less than 10% (Ball and Cope 1961). Traps were operated on five other major spawning tributaries during this period, but no stray fish were captured.

Cutthroat trout in Yellowstone Lake also home for repeat spawning. Cope (1957) tagged 18,836 adults as they entered one of five tributaries to spawn. In subsequent years 244 (1.3%) were recaptured as repeat spawners, and only 8 of these were recaptured in tributaries other than the original. Of the recaptures 96.7% homed.

No in-season homing experiments were done in Yellowstone Lake prior to the present study. However, Platts (1959) conducted such experiments in a high altitude reservoir in Utah. Mature cutthroat trout migrating up tributaries were captured, spawned artificially, tagged, and returned 1.6-6.4 km into the reservoir. Of 2,068 such fish 1,096 (53%) reentered tributaries, and 90% of these chose the initial stream, the rest being recaptured in other tributaries as strays. Apparently the homing motivation was not completely suppressed by stripping of the reproductive products.

Scheer (1939) has reviewed the early work on natal homing of the Atlantic salmon (*Salmo salar*), steelhead trout (*S. gairdneri*), and Pacific salmon (*Oncorhynchus* spp.). Most notable among these studies is that on the sockeye salmon (*O. nerka*) (Clemens et al. 1939). More recent demonstrations of natal homing include: rainbow trout (*S. gairdneri*) (Lindsey et al. 1959), coho salmon (*O. kisutch*) and steelhead trout (Shapovalov and Taft 1954), and brown trout (*S. trutta*) (Stuart 1957). Jones (1959) has reviewed the literature on natal homing of Atlantic salmon. It has been shown that transplanted young pink salmon (O. gorbuscha) (Wickett 1958), coho salmon (Donaldson and Allen 1957), and Atlantic salmon (White and Huntsman 1938) will return at maturity to the tributary where released as young rather than to the stream of parental origin.

Repeat homing occurs in Arctic grayling (Thymallus arcticus) (Kruse 1959), brook trout (Salvelinus fontinalis) (Vladykov 1942), charr (S. willughbii) (Frost 1963), lake trout (S. namaycush) (Eschmeyer 1954, Loftus 1957, Martin 1960), brown trout (Stuart 1957), and rainbow trout (Lindsey et al. 1959).

In-season homing has been demonstrated in brook trout (Vladykov 1942), brown trout (Stuart 1957), charr (Frost 1963), sockeye salmon (Hartman and Raleigh 1964), and pink salmon (Helle 1966). Cutthroat trout (Miller 1954), brook trout (Smith and Saunders 1958), and Dolly Varden (Salvelinus malma) (Armstrong 1965) also home following displacement at times other than the spawning season. Gerking (1959, 1964) has recently reviewed homing in non-salmonid fishes.

Griffin (1952) classified migratory behavior into three categories based on the method used in finding the goal. Hasler et al. (1958) modified the classification as follows: Type I - The ability to find home by use of landmarks in familiar territory and search in unfamiliar territory. Type II - The ability to maintain a constant compass direction in the sense of dead reckoning. Type III - The ability to find home by true navigation involving corrective feedback.

Saila and Shappy (1963) and Patten (1964) proposed two mathematical models of salmon migration in which search on the part of the fish could account for the observed returns. Hasler and Wisby (1958) and Hasler (1956a) have evidence that landmarks may be used in familiar territory. Home water odor may be considered a landmark. Bluntnose minnows (Pimephales notatus) (Hasler and Wisby 1951) and juvenile sockeye salmon (McBride et al. 1964) learned to distinguish between two natural waters by olfaction. Migrating adult sockeye salmon showed olfactory recognition of their home waters by their activity in a tank (Idler et al. 1961, Fagerlund et al. 1963) and chinook salmon (O. tshawytscha) by electroencephalographic responses (Hara et al. 1965). Wisby and Hasler (1954) showed that coho salmon use olfaction to choose between tributaries of a river system.

Jahn (1966) showed that Yellowstone Lake cutthroat trout, displaced westward from their upstream spawning migration to a near shore point or a mid-lake point, displayed a general eastward orientation when continuously tracked for up to two hours. The orientation mechanism was not determined, but the sun may have been used as a reference. Hasler et al. (1958) first demonstrated the sun compass (Type II) orientation in white bass (Roccus chrysops), bluegill (Lepomis macrochirus), and pumpkinseed (L. gibbosus). The roles of sun azimuth, sun altitude, and time compensation in the compass mechanism have been investigated (Braemer 1960, Hasler and Schwassmann 1960, Schwassmann 1960, Schwassmann and Braemer 1961, Braemer and Schwassmann 1963, Schwassmann and Hasler 1964). Winn et al. (1964) demonstrated a sun compass in parrot fishes (Scarus spp.) Johnson and Groot (1963) and Groot (1965) have shown celestial orientation of young sockeye salmon. Henderson (MS 1963) examined the celestial cues available underwater.

Hasler (1956b, 1960a,b, 1966) and Brett and Groot (1963) reviewed the roles of both vision and olfaction in homing. Adler (1963) suggested that organisms do not possess sufficient sensory capabilities for true navigation, but certainly do for compass orientation. Barlow (1964) stated that the possibility of an inertial navigation system in animals should be investigated. While no demonstrations of true navigation in fishes have been made, Neave (1964) feels it must exist, at least in the case of Pacific salmon.

METHODS AND MATERIALS

DESCRIPTION OF STUDY AREA

Yellowstone Lake (Fig. 1) has an area of 354 km^2, a maximum depth of 98 m (42 m mean), and lies at an elevation of 2,358 m msl just east of the continental divide in southeast Yellowstone National Park, Wyoming. Benson (1961) has given basic limnological information for this lake.

Yellowstone Lake is well suited for homing studies, since it is large and has enough tributaries (about 35) to provide adequate choice. This is analagous to the migration of mature salmon from the sea into freshwater streams. It also has an endemic cutthroat trout population, and has not been stocked with trout from other waters.

Release points A, B, and C (Fig. 1) were established equidistant on a line from the mouth of Pelican Creek to the mouth of Clear Creek. Distances (km) from the release points to the stream mouths are as follows:

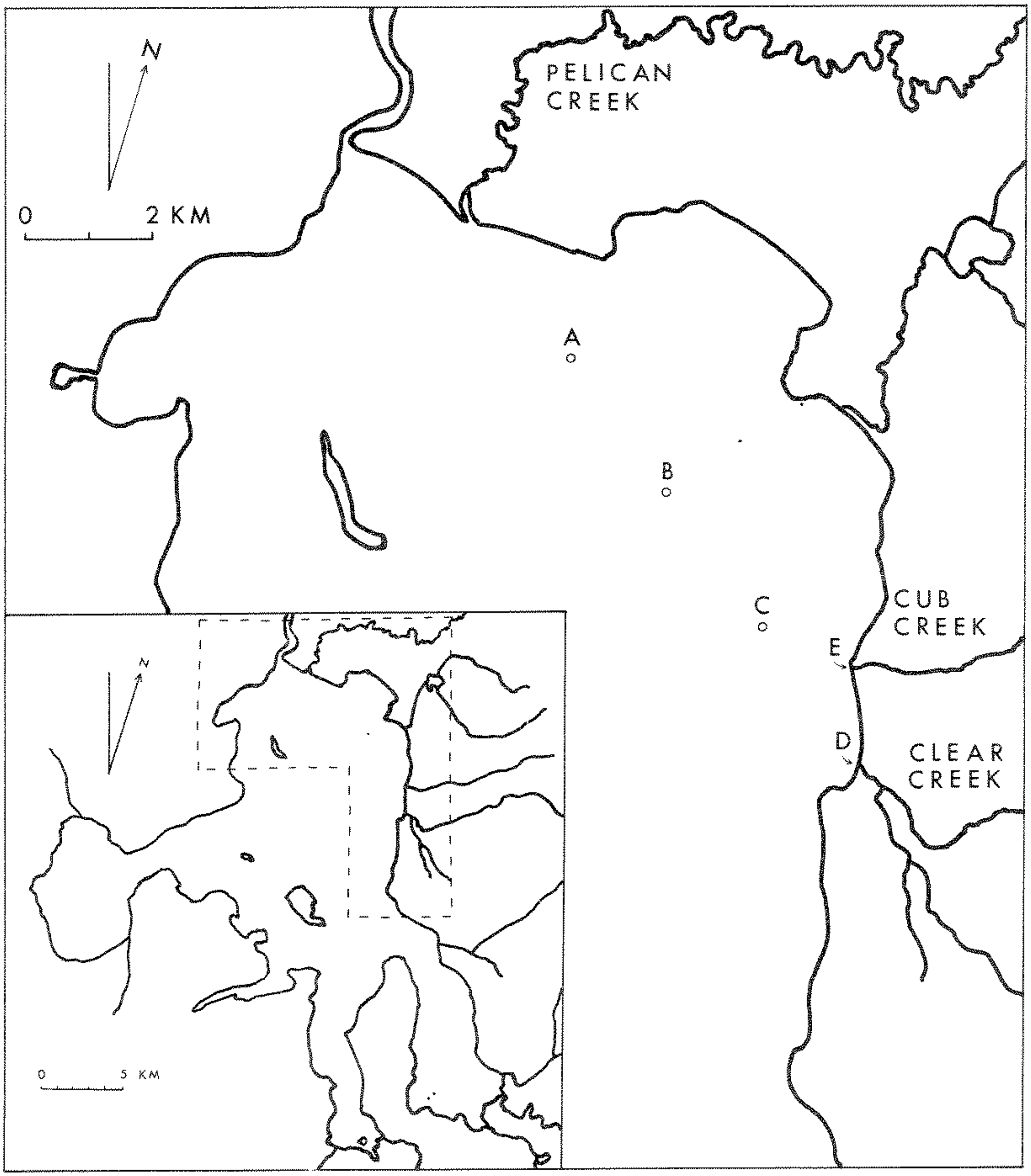

Figure 1. Map of northern portion of Yellowstone Lake showing release points and creeks where experimental cutthroat trout were trapped. Inset shows entire lake and principal tributaries.

	Release Points		
	A	B	C
Mouth of Pelican Creek	2.65	5.30	7.95
Mouth of Clear Creek	7.95	5.30	2.65
Mouth of Cub Creek	6.55	4.00	1.55

In 1964 these points were identified by sighting landmarks with unaided eye each time a release was made. In 1965 and 1966 point B was located with the aid of a sextant and a marker buoy was positioned there. In 1965 points A and C were not used, and in 1966 they were located with the aid of a sextant at the time of each release. Points D and E are in the mouths of Clear and Cub Creeks respectively, and are 1.65 km from one another.

DISPLACEMENT STUDIES

The cutthroat trout used were sexually mature, were moving upstream to spawn, and were collected from the Clear and Cub Creek fish traps. The Clear Creek trap was about 75 m above the stream mouth, and the Cub Creek trap was about 45 m above the mouth in 1964, but about 150 m above in 1965 and 1966, because Cub Creek shifted its course.

In 1964 a few fish at a time were netted from the trap and immediately placed in 15 liters of 1:5000 tricaine methanesulfonate (MS 222: Sandoz Pharmaceuticals) solution. After the fish were anesthetized a numbered monel strap tag (35.0 mm x 3.5 mm) was attached to the posterior edge of the operculum with the aid of a special plier. The total length of each fish was recorded. The sex was also recorded if obvious without extra handling. The fish recovered from the anesthetic after being placed in a covered tub containing 20-25 liters of fresh water. After several fish were tagged the tub was either carried to a boat and the contents emptied into a covered stock tank, or, if the release was to be made at the mouth of the same stream, carried directly to the stream mouth and the fish released. This procedure was repeated until the desired number of fish (10-50) was tagged and either released or placed in the tank. Water was added to make 115-175 liters in the tank. Approximate travel times to release points were as follows (minutes): to point A - 30, point B - 20, point C - 10, and between streams - 8. The maximum time from netting to release was always less than 2 hr, depending on distance to release point and number of fish tagged. Distress of fish at a release point occurred only in two instances. A few fish were not anesthetized and were marked by punching a 6.5 mm hole in the dorsal or caudal fin with a paper punch.

In 1965 and 1966, 5-15 fish were netted from the trap, immediately placed in a covered tub containing 20-25 liters of water, and carried either to the stream mouth or to the stock tank in a boat. This was repeated until the desired number of fish was secured. In 1965, 33-50 fish were released in each group, but in 1966 the number was 25. In addition several extra fish were carried along as spares. It took 16-20 min to reach release point A, 10-13 min to B, 6-8 min to C, and 5-7 min from one stream to the other.

In 1965 and 1966 tagging was done at the release point without anesthetizing or measuring the fish. A 28 mm x 5 mm alligator clip (Minigator: Mueller Co.) was attached to the posterior edge of the dorsal fin at its base with the long axis resting on the dorsal midline of the fish

(McCleave et al. 1967). Release groups were identified in 1965 by a common color code sprayed onto the clips. In 1966 the clips were individually coded by clamping numbered vinyl tubing (Spaghetti FT-4: Floy Tag and Mfg.) inside the prongs which normally clamp a wire. This did not increase the size of the tag but allowed recognition of each fish. Each fish was released immediately after tagging. The maximum time from netting to release was always less than 40 min. Nearly all fish were hauled under relatively calm lake conditions, but occasionally some sloshing of water did occur in the tank.

The fish traps were operated continuously throughout the spawning season except for brief periods of flood conditions. A U. S. Fish and Wildlife Service crew emptied the traps at least once each day, and two or three times when the run was large. All fish were examined for tags. During 1965 and 1966 my colleagues and I usually operated the traps two days each week. Code or tag numbers, date, time, total length, and sex were recorded for all recaptured fish. In addition the U. S. Fish and Wildlife Service periodically electrofished in various portions of the lake and outlet throughout all three summers and all captured trout were examined for tags. A number of tags were returned by anglers although their help was not solicited.

During 1966 releases were also made of tagged blinded, olfactory occluded (anosmic), and anesthetized controls, using the same general procedure as with the previously described 1966 releases.

At release point B, 1-5 fish at a time were anesthetized (1.0-1.5 min) in 1:7500 MS 222 solution. Fish were blinded by injecting 0.10-0.15

cm^3 of 3% aqueous benzethonium chloride (Phemerol: Parke Davis and Co.) into the eyeball. The eye became opaque and turned green immediately, and after several hours changed to white. Plugging of the nares was done with melted distilled acetylated monoglycerides (Myvacet, Type 5-00: Distillation Products Industries, Eastman Kodak Co.) (Bardach and Case 1965). The warmed material (which is liquid above 43° C) was injected from a veterinary syringe using a blunt needle into either the anterior or posterior naris on each side until it began to flow from the other naris. It immediately congealed into a tough, waxy solid which blocked water passage. Each fish was tagged with a numbered alligator clip and placed in a tub containing 25-30 liters of fresh water for a period of 4-7 min, and then released. Time from netting to release was less than 58 min for blind fish, less than 73 min for anosmic fish, and less than 45 min for control fish. Equal numbers of blind and control fish were released on one day, and equal numbers of anosmic and control fish were released on a different day. The heads of all recaptured anosmic fish were preserved for examination of the olfactory plugs.

FLOAT-TRACKING STUDIES

The polystyrene foam (Styrofoam: Dow Chemical Co.) float-tracking method described by Jahn (1966) was used to determine direction of "take-off" of mature, migrating cutthroat trout displaced from tributaries to point B. The floats were Styrofoam cubes 5 cm on a side wrapped with aluminum foil. Each of these was connected by a 2 m nylon thread to an alligator clip used to attach the device to the dorsal fin. Four experimental groups of trout were tracked: blind (anesthetized and blinded), anosmic (anesthetized and olfactory occluded), control (anesthetized only), and non-anesthetized. Blind, control, and non-anesthetized Cub Creek trout and blind, anosmic, and control Clear Creek trout were tracked in 1965. Blind, anosmic, and control Clear, Cub, and Pelican Creek trout were tracked in 1966.

In 1965, 8-12 trout were netted from the traps and carried in two covered tubs of 20-30 liters water to the boat and either placed in the boat or emptied into a covered stock tank for transportation. Non-anesthetized trout were transported to point B, the floats attached, and 10 individuals released with as little handling as possible. All trout for the olfaction experiment were taken to point B and anesthetized in 1:7500 MS 222 solution. The nares of half of these were plugged using cotton soaked in Phemerol. Trout were allowed to recover in fresh water and then floats attached. Five anosmic and five control trout were released. Trout for the blinding experiments were treated in one of three ways. Most were hauled in tubs or a stock tank just offshore from the collection stream and anesthetized. Half of these were blinded by Phemerol injection and all were allowed to recover during the rest of the trip to point B. On one occasion several Clear Creek trout were hauled to the release point prior to anesthetizing and blinding. On two other occasions Clear Creek trout were anesthetized at the trap site and half of them were blinded. All were placed in a live box for recovery, one group for 91 hr, the other for 19 hr, prior to transportation to point B. Either four blind and four control trout or three blind and three control trout were released for each experiment.

In 1966, 4-10 trout were removed from the Clear, Cub, and Pelican Creek traps and carried to the boat. The Pelican Creek trap, about 2 km upstream from the mouth, was not very effective because of flood damage, but enough trout were captured for float-tracking experiments. Pelican Creek trout were transported in 35-40 liters of water by truck 4.4 km (about 5 min) to the boat, and Clear and Cub Creek trout were transported as in 1965. Just offshore the trout were anesthetized. Some were blinded with Phemerol, some plugged with either white petroleum jelly injected through a needleless syringe or with warmed Myvacet, and some simply placed back in fresh water. All were allowed to recover on the remainder of the trip to point B. Usually six trout (two blind, two anosmic, two control) were released at a time, but on one occasion only one of each kind was released. With the exception of those blind trout held in the live box the time from netting to release was always less than 90 min and usually less than 70 min.

Trout with attached floats were released individually, and sufficient time was allowed between releases to reduce the possibility of the floats becoming entangled. In all but the initial five 1965 experiments a drift drogue (Jahn 1966) suspended at 1 m was released as soon as the last fish had cleared the release area. After experimental fish had been at large for an average of 1 hr, they were picked up as quickly as possible. A large, stable azimuth sighting compass was used to obtain a bearing (to the nearest degree) from the fish to the release buoy. Distance to the buoy was not measured. After each sighting an attempt was made to pick up the trout for length measurement, sex determination, and in 1966 also for tagging with a numbered alligator clip. Nearly all fish were picked up, but a few pulled loose from the float or were not found before the termination of the experiment. A bearing from the drogue to the buoy was taken and the drogue recovered.

In 1965 one control trout, one blind trout and in 1966 one non-anesthetized trout (all from Clear Creek) were float-tracked individually from Point B for longer periods (3 hr 26 min-6 hr 20 min). These fish were subjected to the same treatment as groups in the short term experiments described previously. Sextant sightings of landmarks were used to make position plots at 15-45 min intervals depending on how far the fish moved. All experiments were terminated when the lake surface became so rough that accurate position plots were impossible.

STATISTICAL ANALYSES

Displacement Studies. Chi-square analyses were used to compare the numbers of trout recaptured from various releases. Expected numbers of fish in each cell of the Chi-square computation formula were obtained by multiplying the percent recapture of all release groups in the comparison by the number of fish in each release group.

The time from release to recapture among various release groups was compared using an analysis of variance for unequal sample sizes (Steel and Torrie 1960). Since the distribution of time to recapture (in hours) was skewed toward the longer times, each time value was transformed to its square root. All statistical analyses were performed on transformed data, but the mean time values are presented in hours. The adjusted mean is the square of the mean of the transformed data. If the analyses of variance did not yield significant F values, Bartlett's test for homogeneity of variance (Bartlett 1937a,b) was done as a further check on the assumptions of the analysis of variance model. If more than two release groups were compared in any analysis of variance, Duncan's new multiple-range test (Duncan 1955) was performed on the ranked means of the transformed data to compare all pairs of means.

Float-Tracking Studies. The observed directions from the release buoy to float-tracked trout were represented as points of equal mass on the circumference of a unit circle. An empirical mean vector pointing to the center of mass of the distribution of each group of fish was calculated with polar coordinates *r* (length) and *a* (angle) (Batschelet 1965). The Rayleigh test (Greenwood and Durand 1955) for a significant *r* value was then used. If *r* was significantly greater than zero, the null hypothesis of a uniform circular distribution was rejected. A resultant vector F test (Watson and Williams 1956) was used to compare the mean directions (*a*) of two groups of tracked trout. Another test statistic, R, based on a resultant vector (Watson and Williams 1956, Stephens 1962) was used to determine if the mean direction (*a*) of a group of trout was significantly different from the homestream direction. A concise discussion of all these methods is given by Batschelet (1965).

RESULTS

DISPLACEMENT STUDIES

Tagging and displacement of 1,137 Clear Creek and 771 Cub Creek cutthroat trout were done from 15-27 July 1964, 7-17 July 1965, and 27 June-13 July 1966. A summary of displacement and recapture is shown in Table I, and Chi-square values for certain comparisons are shown in Table II.

Clear Creek trout homed about equally well in 1965 and 1966 and significantly better in both years than in 1964. The same was true of Cub Creek trout. Straying of both Clear and Cub Creek trout was greater in 1965 and 1966 than in 1964, but in the case of 1965 Clear Creek trout the difference was not significant. Straying was about equal among Cub Creek trout in 1965 and 1966, but among Clear Creek trout it was greater in 1966 than in 1965. Total recapture percentages (including angler returns) for both streams were about equal in 1965 and 1966, and were greater than in 1964. The percentage of trout homing was significantly greater than the percentage straying in all three years for both streams.

In 1964 Cub Creek trout homed in significantly greater percentage than Clear Creek trout, but in 1965 and 1966 the reverse was true. In all three years Cub Creek trout strayed significantly more than Clear Creek trout. In 1964 the total percent recapture of Cub Creek trout was greater than that of Clear Creek trout. In 1965 and 1966 total recaptures of the two streams showed a non-significant difference of less than 2%.

In 1966 Clear and Cub Creek trout were displaced to all release points. No significant differences in homing were found among releases at open-water points, or were any trends evident. Trout displaced to the

Table I. Summary of displacement and recapture of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966. (Percentages in parentheses. Discrepancies in row percentage sums result from rounding numbers.)

Origin stream	Year	Release point	Number released	Number of recaptures: Homing	Straying	Angling	Total
Clear	1964	A	35	4(11.4)a/	1 (2.9)	1 (2.9)	6(17.1)
		B	150	7 (4.7)	1 (0.7)	2 (1.3)	10 (6.7)
		C	158	18(11.4)b/	2 (1.3)	3 (1.9)c/	23(14.6)
		Mouth Clear Cr.	20	3(15.0)	0 (0.0)	1 (5.0)	4(20.0)
		Total	363	32 (8.8)	4 (1.1)	7 (1.9)	43(11.8)
Cub	1964	B	20	4(20.0)	0 (0.0)	1 (5.0)	5(25.0)
		C	106	19(17.9)	5 (4.7)	3 (2.8)	27(25.5)
		Mouth Cub Cr.	10	1(10.0)	1(10.0)	0 (0.0)	2(20.0)
		Mouth Clear Cr.	10	4(40.0)	1(10.0)	1(10.0)c/	6(60.0)
		Total	146	28(19.2)	7 (4.8)	5 (3.4)	40(27.4)
Total	1964	All points combined	509	60(11.8)	11 (2.2)	12 (2.4)	83(16.3)
Clear	1965	B	274	122(44.5)	7 (2.6)	2 (0.7)	131(47.8)
		Inside Mouth Clear Cr.	50	24(48.0)	0 (0.0)	0 (0.0)	24(48.0)
		Outside Mouth Clear Cr.	50	24(48.0)	0 (0.0)	0 (0.0)	24(48.0)
		Total	374	170(45.5)	7 (1.9)	2 (0.5)	179(47.9)
Cub	1965	B	175	57(32.6)	27(15.4)	1 (0.6)	85(48.6)
		Inside Mouth Cub Cr.	25	9(36.0)	0 (0.0)	0 (0.0)	9(36.0)
		Outside Mouth Cub Cr.	25	9(36.0)	2 (8.0)	0 (0.0)	11(44.0)
		Total	225	75(33.3)	29(12.9)	1 (0.4)	105(46.7)
Total	1965	All points combined	599	245(40.9)	36 (6.0)	3 (0.5)	284(47.4)

Table I. Continued.

Origin stream	Year	Release point	Number released	Number of recaptures: Homing	Straying	Angling	Total
Clear	1966	A	100	45(45.0)	2 (2.0)	3 (3.0)[d]	50(50.0)
		B	100	43(43.0)	5 (5.0)	1 (1.0)	49(49.0)
		C	100	42(42.0)	5 (5.0)	1 (1.0)	48(48.0)
		Mouth Clear Cr.	50	24(48.0)	3 (6.0)	0 (0.0)	27(54.0)
		Mouth Cub Cr.	50	20(40.0)	3 (6.0)	1 (2.0)	24(48.0)
		Total	400	174(43.5)	18 (4.5)	6 (1.5)	198(49.5)
Cub	1966	A	100	30(30.0)	12(12.0)	1 (1.0)	43(43.0)
		B	100	27(27.0)	9 (9.0)	2 (2.0)	38(38.0)
		C	100	34(34.0)	20(20.0)	2 (2.0)	56(56.0)
		Mouth Clear Cr.	50	17(34.0)	11(22.0)	1 (2.0)	29(58.0)
		Mouth Cub Cr.	50	27(54.0)	2 (4.0)	1 (2.0)	30(60.0)
		Total	400	135(33.8)	54(13.5)	7 (1.8)	196(49.0)
Total	1966	All points combined	800	309(38.6)	72 (9.0)	13 (1.6)	394(49.3)
Grand total	All years	All streams combined	1908	614(32.2)	119 (6.2)	28 (1.5)	761(39.0)

a/ Includes one fish recaptured in 1966.

b/ Includes one fish recaptured in 1965 and one fish recaptured in 1966.

c/ Includes one fish recaptured in home stream previously.

d/ Includes one fish recaptured by electrofishing.

Table II. Chi-square comparisons of the recaptures of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966. (Total categories include angler returns. With 1 d.f. 95% Chi-square = 3.84, 99% Chi-square = 6.63.)

Origin stream	Year	Release point(s)	Recapture category	v.	Origin stream	Year	Release point(s)	Recapture category	Chi-square
Clear	1964	Combined	Home		Clear	1965	Combined	Home	90.24**
	1964					1966			84.78**
	1965					1966			0.17
	1964		Stray			1965		Stray	0.74
	1964					1966			7.62**
	1965					1966			4.14*
	1964		Total			1965		Total	79.33**
	1964					1966			85.41**
	1965					1966			0.11
Cub	1964	Combined	Home		Cub	1965	Combined	Home	6.39*
	1964					1966			7.61**
	1965					1966			0.01
	1964		Stray			1965		Stray	5.97*
	1964					1966			7.36**
	1965					1966			0.04
	1964		Total			1965		Total	8.41**
	1964					1966			11.55**
	1965					1966			0.16
Clear	1964	Combined	Home		Clear	1964	Combined	Stray	21.80**
	1965					1965			150.10**
	1966					1966			126.76**
Cub	1964	Combined	Home		Cub	1964	Combined	Stray	12.60**
	1965					1965			20.34**
	1966					1966			34.72**

Table II. Continued.

Origin stream	Year	Release point(s)	Recapture category	v.	Origin stream	Year	Release point(s)	Recapture category	Chi-square
Clear	1964	Combined	Home		Cub	1964	Combined	Home	9.48**
			Stray					Stray	6.56*
			Total					Total	15.45**
Clear	1965	Combined	Home		Cub	1965	Combined	Home	5.05*
			Stray					Stray	28.38**
			Total					Total	0.04
Clear	1966	Combined	Home		Cub	1966	Combined	Home	4.92*
			Stray					Stray	18.00**
			Total					Total	0.01
Clear	1966	A	Home		Clear	1966	B	Home	0.05
		A					C		0.10
		A					Mouth Clear Cr.		0.07
		A					Mouth Cub Cr.		0.19
		B					C		0.01
		B					Mouth Clear Cr.		0.19
		B					Mouth Cub Cr.		0.07
		C					Mouth Clear Cr.		0.27
		C					Mouth Cub Cr.		0.03
		Mouth Clear Cr.					Mouth Cub Cr.		0.36
Cub	1966	A	Home		Cub	1966	B	Home	0.16
		A					C		0.25
		A					Mouth Cub Cr.		5.05*
		A					Mouth Clear Cr.		0.17
		B					C		0.80
		B					Mouth Cub Cr.		6.75**
		B					Mouth Clear Cr.		0.56
		C					Mouth Cub Cr.		3.35
		C					Mouth Clear Cr.		0.00
		Mouth Cub Cr.					Mouth Clear Cr.		2.27

Table II. Continued.

Origin stream	Year	Release point(s)	Recapture category	v.	Origin stream	Year	Release point(s)	Recapture category	Chi-square
Clear	1964	Mouth Clear Cr.	Home		Clear	1964	Open-water points	Home	0.92
	1965					1965			0.19
	1966					1966			0.23
	Comb.					Comb.			7.94**
Cub	1964	Mouth Cub Cr.	Home		Cub	1964	Open-water points	Home	4.47*
	1965					1965			3.26
	1966					1966			7.10**
	Comb.					Comb.			5.45*

* Significant at 95% level.
** Significant at 99% level.

opposite stream mouth and to open-water homed about equally well. Homing from the mouths of the origin streams was usually greater than from the other release points.

In 1964, 1965, and 1966 homing to Clear Creek from the mouth of Clear Creek was greater than from all open-water points combined, but was significantly greater only if all three years were combined. Homing to Cub Creek from the mouth of Cub Creek was significantly less in 1964, slightly greater in 1965, and significantly greater in 1966, than from the combined open-water points. In 1965 Clear and Cub Creek trout were released 5-10 m outside or 5-10 m inside the origin stream mouth. Homing performance was the same from inside and outside the mouth.

A summary of the displacement and recapture in 1964 of Clear and Cub Creek trout of known sex is shown in Table III. There was no significant difference between the recapture of males and females in any category.

In 1964, 47 opercle-tagged trout and 39 fin-punched trout were displaced from Cub Creek to point C. Six (12.8%) of the tagged trout and 8 (20.5%) of the punched trout homed. One (2.1%) of the tagged trout and 3 (7.7%) of the punched trout strayed. Although a higher percentage of punched trout than tagged trout homed, and a higher percentage strayed, Chi-square values for homing (0.79) and straying (1.42) were non-significant.

Times from release to recapture of 390 Clear Creek trout and 311 Cub Creek trout displaced during 1964, 1965, and 1966 are given in Table IV. Analyses of variance of the mean homing times of these trout from various release points are given in Table V and Duncan's new multiple-range com-

Table III. Displacement and recapture of trout of known sex from Clear and Cub Creeks, 15-27 July 1964. (With 1 d.f. 95% Chi-square = 3.84, 99% Chi-square = 6.63.)

Origin Stream:	Clear Creek		Cub Creek		Combined	
Sex:	♂	♀	♂	♀	♂	♀
Number released	120	107	27	37	147	144
Homing: Number	14[a]	10	3	6	17	16
Percent	11.7	9.3	11.1	16.2	11.6	11.1
Chi-square	0.48		0.29		0.13	
Straying: Number	2	0	0	2	2	2
Percent	1.7	0.0	0.0	5.4	1.4	1.4
Chi-square	1.96		1.46		0.00	
Angling: Number	5[a]	1	2	2	7	3
Percent	4.2	0.9	7.4	5.4	4.8	2.1
Chi-square	2.48		1.00		1.52	
Total: Number	21[a]	11	5	10	26	21
Percent	17.5	10.3	18.5	27.0	17.7	14.6
Chi-square	2.50		0.48		0.43	

a/ Includes one fish counted as both homing and angling.

parisons of the homing times in Table VI. Straying times were not statistically treated due to small samples.

In 1964 no patterns were evident among Clear and Cub Creek trout displaced to the various open-water release points. Homing time from the mouths of the origin streams was less than from open-water points, and significantly so in the case of Clear Creek trout returning from points A and C. In 1965 Clear Creek trout released 5-10 m inside the mouth of Clear Creek homed significantly faster than those released either 5-10 m outside the mouth or at point B. No significant differences in homing times were found in 1965 Cub Creek trout. In 1966 a pattern in adjusted mean homing times was exhibited by both Clear and Cub Creek trout. Homing times were inversely related to distance for all points (except the oppo-

Table IV. Time (hr) from release to recapture of displaced Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966.

			Homing				Straying			
Year	Origin stream	Release point	Mean time	Adjusted mean time	Time range	Sample size	Mean time	Adjusted mean time	Time range	Sample size
1964	Clear	A	116.7	111.8	69-184	3	58.0	58.0	58	1
		B	57.9	53.9	15-104	7	121.0	121.0	121	1
		C	69.7	65.0	25-142	16	32.0	30.8	20- 44	2
		Mouth Clear	35.0	16.4	1-103	3				0
1964	Cub	B	52.3	51.6	34- 59	4				0
		C	42.3	40.5	23- 71	10	49.0	45.3	23- 75	2
		Mouth Cub	34.0	34.0	34	1	34.0	34.0	34	1
		Mouth Clear	70.8	70.5	58- 75	4	32.0	32.0	32	1
1965	Clear	B	99.1	91.7	8-432	118	118.1	112.0	55-200	7
		Mouth Clear (In)	60.7	45.7	5-409	24				0
		Mouth Clear (Out)	121.2	105.8	6-599	21				0
	Cub	B	86.2	82.0	34-198	56	109.0	94.3	10-343	25
		Mouth Cub (In)	90.6	85.2	32-152	9				0
		Mouth Cub (Out)	71.2	67.1	32-151	9	39.5	38.8	29- 50	2
1966	Clear	A	103.3	96.0	12-272	45	33.0	33.0	33	2
		B	126.8	113.6	8-297	42	134.5	122.1	33-243	4
		C	126.6	118.2	31-308	42	58.4	49.7	6-127	5
		Mouth Clear	164.5	154.7	27-268	23	115.0	99.7	28-221	3
		Mouth Cub	158.6	150.2	73-337	18	162.3	158.0	93-201	3
	Cub	A	108.9	101.6	31-296	29	100.5	90.9	33-200	12
		B	122.6	111.0	26-363	27	107.4	101.1	32-174	8
		C	139.6	127.4	30-462	34	98.1	84.5	6-241	20
		Mouth Clear	146.8	138.5	30-296	18	71.0	50.6	3-196	10
		Mouth Cub	136.8	132.3	58-272	27	126.5	125.3	102-151	2

Table V. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time of Clear and Cub Creek trout from various release points in 1964, 1965, and 1966. (Figures in parentheses are 95% and 99%, respectively, significance values with appropriate d.f. for both F and Chi-square tests.)

Source of variation	d.f.	Sum of squares	Mean square	F	Bartlett's test: Chi-square
1964 Clear Creek trout					
Between release points	3	68.08	22.69	3.29*	-
Within release points	25	172.14	6.89	(2.99-	
Total	28	240.22		4.68)	
1964 Cub Creek trout					
Between release points	3	13.27	4.42	31.6	3.47
Within release points	15	20.97	1.40	(3.29-	(7.81-
Total	18	34.24		5.42)	11.30)
1965 Clear Creek trout					
Between release points	2	183.82	91.91	9.40**	-
Within release points	160	1564.90	9.78	(3.06-	
Total	162	1748.72		4.74)	
1965 Cub Creek trout					
Between release points	2	6.41	3.21	<1	0.29
Within release points	71	323.48	4.56	(3.13-	(5.99-
Total	73	329.89		4.92)	9.21)
1966 Clear Creek trout					
Between release points	4	144.84	36.21	3.71**	-
Within release points	165	1609.59	9.76	(2.42-	
Total	169	1754.43		3.43)	
1966 Cub Creek trout					
Between release points	4	50.84	12.71	1.36	8.09
Within release points	130	1213.06	9.33	(2.44-	(9.49-
Total	134	1263.90		3.47)	13.28)

* Significant at 95% level.
** Significant at 99% level.

site stream mouth): trout released at the farthest point (A) homed the fastest and those at the mouth of the origin stream the slowest. The analysis of variance was significant for Clear Creek trout, but Duncan's test showed significance only between releases at point A and the mouth of

Table VI. Duncan's new multiple-range comparisons of the mean homing time of Clear and Cub Creek trout from various release points in 1964, 1965, and 1966.

Comparison between		Difference between means	Least significant range 95%	Least significant range 99%
1964 Clear Creek trout				
A	C	2.51	3.41	4.61
A	B	3.23	3.93	5.29
A	Mouth Clear	6.52**	4.77	6.41
C	B	0.72	2.46	3.32
C	Mouth Clear	4.02*	3.59	4.82
B	Mouth Clear	3.30	3.74	5.06
1964 Cub Creek trout				
Mouth Clear	B	1.21	1.78	2.47
Mouth Clear	C	2.03*	1.56	2.16
Mouth Clear	Mouth Cub	2.57	3.04	4.21
B	C	0.82	1.49	2.06
B	Mouth Cub	1.35	2.96	4.09
C	Mouth Cub	0.54	2.64	3.66
1965 Clear Creek trout				
Mouth Clear (Out)	B	0.71	1.48	1.97
Mouth Clear (Out)	Mouth Clear (In)	3.52**	1.97	2.59
B	Mouth Clear (In)	2.81**	1.40	1.86
1965 Cub Creek trout				
Mouth Cub (In)	B	0.18	1.53	2.04
Mouth Cub (In)	Mouth Cub (Out)	1.04	2.12	2.79
B	Mouth Cub (Out)	0.86	1.53	2.04
1966 Clear Creek trout				
Mouth Clear	Mouth Cub	0.18	2.75	3.64
Mouth Clear	C	1.57	2.38	3.12
Mouth Clear	B	1.78	2.46	3.22
Mouth Clear	A	2.64*	2.49	3.24
Mouth Cub	C	1.38	2.46	3.26
Mouth Cub	B	1.60	2.59	3.39
Mouth Cub	A	2.46	2.65	3.46
C	B	0.22	1.90	2.52
C	A	1.08	1.39	1.82
B	A	0.86	1.32	1.75

Table VI. Continued.

Comparison between		Difference between means	Least significant range 95%	99%
1966 Cub Creek trout				
Mouth Clear	Mouth Cub	0.27	1.84	2.43
Mouth Clear	C	0.48	1.86	2.43
Mouth Clear	B	1.24	1.99	2.60
Mouth Clear	A	1.69	2.02	2.62
Mouth Cub	C	0.21	1.56	2.06
Mouth Cub	B	0.97	1.73	2.27
Mouth Cub	A	1.42	1.76	2.29
C	B	0.75	1.56	2.06
C	A	1.21	1.61	2.11
B	A	0.45	1.62	2.14

* Significant at 95% level.
** Significant at 99% level.

Clear Creek. Neither the analysis of variance nor Duncan's test was significant for Cub Creek trout, but the pattern was consistent. Those trout released at the mouths of the opposite streams homed in about equal time to those from the mouths of the origin streams.

There were no significant differences in the mean homing times between Clear and Cub Creek trout from open-water points in 1964, 1965, and 1966, except in 1964 Cub Creek trout homed faster than Clear Creek trout from point C (Table VII). However the assumption of homogeneous variance was not met in the case of 1965 point B releases. Cub Creek trout did not home consistently faster than Clear Creek trout even though Cub Creek is nearer to the open-water release points.

Clear and Cub Creek trout homed significantly faster from point B in 1965 than in 1966 (Table VIII). Homing times in 1964 were not compared

Table VII. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time between Clear and Cub Creek trout from open-water points in 1964, 1965, and 1966. (Figures in parentheses are 95% and 99%, respectively, significance values with appropriate d.f. for both F and Chi-square tests.)

Source of variation	d.f.	Sum of squares	Mean square	F	Bartlett's test: Chi-square
1964 Point B releases					
Between creeks	1	0.07	0.07	<1	2.26
Within creeks	9	29.81	3.31	(5.12-	(3.84-
Total	10	29.88		10.56)	6.63)
1964 Point C releases					
Between creeks	1	17.75	17.75	4.62*	-
Within creeks	24	92.07	3.84	(4.26-	
Total	25	109.82		7.82)	
1965 Point B releases					
Between creeks	1	10.30	10.30	1.58	5.22*
Within creeks	172	1118.46	6.50	(3.90-	(3.84-
Total	173	1128.76		6.79)	6.63)
1966 Point A releases					
Between creeks	1	1.40	1.40	<1	0.00
Within creeks	72	540.98	7.51	(3.98-	(3.84-
Total	73	542.38		7.01)	6.63)
1966 Point B releases					
Between creeks	1	0.27	0.27	<1	0.13
Within creeks	67	870.01	12.99	(3.98-	(3.84-
Total	68	870.28		7.01)	6.63)
1966 Point C releases					
Between creeks	1	3.22	3.22	<1	1.39
Within creeks	74	764.35	10.33	(3.97-	(3.84-
Total	75	767.57		6.99)	6.63)

* Significant at 95% level.

statistically with 1965 and 1966 due to different tagging procedures, but in 1964 homing times were considerably less than in 1965 and 1966.

Homing times from open-water points were recorded for 76 males and 162 females from Clear Creek and 32 males and 113 females from Cub Creek in 1965 and 1966 (Table IX). Homing times were usually the same for males

Table VIII. Analysis of variance of the mean homing time between 1965 and 1966 Clear and Cub Creek trout displaced to point B. (Figures in parentheses are 95% and 99%, respectively, significance values with appropriate d.f. for F tests.)

Source of variation	d.f.	Sum of squares	Mean square	F
Clear Creek fish				
Between years	1	36.33	36.33	4.00*
Within years	158	1434.66	9.08	(3.91-
Total	159	1470.99		6.80)
Cub Creek fish				
Between years	1	40.05	40.05	5.86*
Within years	81	553.67	6.84	(3.96-
Total	82	593.72		6.96)

* Significant at the 95% level.

and females. Analyses of variance (Table X) showed no significant differences between the sexes in any release group, although in one instance the assumption of homogeneous variance was not met.

The results of experiments involving 50 blind, 50 anosmic, and two groups (A and B) of 50 control trout displaced from Clear Creek to point B in 1966 are given in Table XI. The performance of two groups (A and B) of 25 non-anesthetized trout already included in other experiments are used for comparison with the blind, anosmic, and control groups, which were all anesthetized prior to tagging.

There were no significant differences in the percentages of trout homing among the release groups, although a slightly greater percentage of non-anesthetized trout homed. The anosmic, control B, and non-anesthetized B groups strayed more, but not significantly so, than the three groups released 7-9 days earlier. The total recapture percentages

Table IX. Time (hr) from release to recapture in the homestream of male amd female trout displaced from Clear and Cub Creeks to open-water points during 1965 and 1966.

Year	Origin stream	Release point	Sex	Mean time	Adjusted mean time	Time range	Sample size
1965	Clear	B	♂	100.9	95.3	8-202	32
			♀	103.3	93.8	8-366	81
	Cub	B	♂	90.1	87.8	54-177	15
			♀	84.9	79.8	34-198	40
1966	Clear	A	♂	108.0	102.9	34-224	17
			♀	103.8	96.6	34-272	27
		B	♂	111.9	97.8	8-223	16
			♀	133.4	121.0	32-297	25
		C	♂	105.0	100.5	50-191	11
			♀	131.3	121.7	31-308	29
	Cub	A	♂	124.9	116.7	32-199	7
			♀	103.8	97.0	32-296	22
		B	♂	166.2	159.3	79-294	5
			♀	112.7	101.2	26-363	22
		C	♂	149.8	148.2	102-174	5
			♀	137.9	124.0	30-462	29

of all groups were not significantly different. Thus blind trout were able to home as well as control trout, and anesthetization *per se* affected homing performance only slightly if at all. Thirty anosmic trout were recaptured, but 22 had lost one or both nasal plugs. Of these 16 homed and 6 strayed. Of the 8 whose plugs were intact, 7 homed, 1 strayed.

Mean homing times of one blind, one anosmic, two control, and two non-anesthetized groups of trout are given in Table XII. The analysis of variance of the differences in the homing times was significant (Table XIII). Duncan's new multiple-range comparisons (Table XIV) showed that the blind, control A, and non-anesthetized A groups all homed significant-

Table X. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing time of male and female Clear and Cub Creek trout displaced to open-water points during late June and July, 1965 and 1966. (Figures in parentheses are 95% F values for appropriate d.f. With 1 d.f. 95% Chi-square = 3.84, 99% Chi-square = 6.63.)

Source of variation	d.f.	Sum of squares	Mean square	F	Bartlett's test: Chi-square
1965 Clear Cr. - Point B					
Between sexes	1	0.14	0.14	<1	2.65
Within sexes	111	945.00	8.51	(3.93)	
Total	112	945.14			
1965 Cub Cr. - Point B					
Between sexes	1	2.07	2.07	<1	2.47
Within sexes	53	236.58	4.46	(4.03)	
Total	54	238.65			
1966 Clear Cr. - Point A					
Between sexes	1	1.01	1.01	<1	0.40
Within sexes	42	280.28	6.67	(4.07)	
Total	43	281.29			
1966 Clear Cr. - Point B					
Between sexes	1	12.04	12.04	<1	0.05
Within sexes	39	533.51	13.68	(4.09)	
Total	40	545.55			
1966 Clear Cr. - Point C					
Between sexes	1	8.12	8.12	<1	1.80
Within sexes	38	327.72	8.62	(4.10)	
Total	39	335.84			
1966 Cub Cr. - Point A					
Between sexes	1	4.82	4.82	<1	0.20
Within sexes	27	206.59	7.65	(4.21)	
Total	28	211.41			
1966 Cub Cr. - Point B					
Between sexes	1	26.72	26.72	2.32	0.65
Within sexes	25	288.60	11.54	(4.24)	
Total	26	315.32			
1966 Cub Cr. - Point C					
Between sexes	1	4.60	4.60	<1	3.88*
Within sexes	32	410.98	12.84	(4.15)	
Total	33	415.58			

* Significant at 95% level.

Table XI. Results of displacement of blind, anosmic, control, and non-anesthetized trout from Clear Creek to point B, 1966. (Percentages in parentheses. With 5 d.f. 95% Chi-square = 11.1, 99% Chi-square = 15.1.)

Release date	Experimental group	Number released	Number of recaptures		
			Homing	Straying	Total
4 July	Non-anesthetized A	25	14(56)	1(4)	15(60)
5 July	Control A	50	25(50)	2(4)	27(54)
5 July	Blind	50	25(50)	3(6)	28(56)
12 July	Anosmic	50	23(46)	7(14)	30(60)
12 July	Control B	50	16(32)	5(10)	21(42)
13 July	Non-anesthetized B	25	13(52)	2(8)	15(60)
Chi-square			3.18	4.25	2.01

Table XII. Time (hr) from release to recapture in the homestream of blind, anosmic, control, and non-anesthetized Clear Creek trout displaced to point B, 1966.

Release date	Experimental group	Mean time	Adjusted mean time	Time range	Sample size
4 July	Non-anesthetized A	148.2	139.8	34-271	14
5 July	Control A	114.7	108.7	10-200	25
5 July	Blind	237.8	222.3	78-479	25
12 July	Anosmic	63.5	58.4	27-174	23
12 July	Control B	66.6	63.4	27-126	16
13 July	Non-anesthetized B	60.7	52.7	8-126	12
Anosmic	Plugs intact	74.6	71.6	30-125	7
Anosmic	1-2 plugs lost	58.8	53.1	27-174	16

ly slower than the anosmic, control B, and non-anesthetized B groups which were released at a later time. The blind trout were also significantly slower than the control A and non-anesthetized A groups. The anosmic group homed in about the same length of time as the control B and non-anesthetized B groups. The homing times of non-anesthetized groups were not significantly different from comparable control groups, so anesthetization *per se* had no effect on the homing time. The mean homing time

Table XIII. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing times of blind, anosmic, control, and non-anesthetized trout from Clear Creek displaced to point B, 1966. (Figures in parentheses are 95% and 99%, respectively, significance values with appropriate d.f. for F tests. With 1 d.f. 95% Chi-square = 3.84.)

Source of variation	d.f.	Sum of squares	Mean square	F	Bartlett's test: Chi-square
All groups analysis					
Between groups	5	924.55	184.91	21.91**	-
Within groups	109	920.27	8.44	(2.30-	
Total	114	1844.82		3.19)	
Anosmic group: Intact v. lost plugs					
Between groups	1	6.77	6.77	1.27	0.63
Within groups	21	111.65	5.32	(4.32-	
Total	22	118.42		8.02)	

** Significant at 99% level.

Table XIV. Duncan's new multiple-range comparisons of the mean homing times of blind, anosmic, control, and non-anesthetized trout from Clear Creek displaced to point B, 1966.

Comparison between		Difference between means	Least significant range 95%	Least significant range 99%
Blind	Non-anesthetized A	3.08**	1.92	2.54
Blind	Control A	4.49**	1.71	2.24
Blind	Control B	6.94**	2.01	2.62
Blind	Anosmic	7.27**	1.85	2.41
Blind	Non-anesthetized B	7.65**	2.30	2.97
Non-anesthetized A	Control A	1.40	1.92	2.54
Non-anesthetized A	Control B	3.86**	2.22	2.90
Non-anesthetized A	Anosmic	4.18**	2.12	2.77
Non-anesthetized A	Non-anesthetized B	4.56**	2.52	3.28
Control A	Control B	2.45**	1.84	2.44
Control A	Anosmic	2.78**	1.75	2.29
Control A	Non-anesthetized B	3.16**	2.20	2.87
Control B	Anosmic	0.32	1.87	2.48
Control B	Non-anesthetized B	0.70	2.32	3.03
Anosmic	Non-anesthetized B	0.38	2.05	2.71

** Significant at 99% level.

of the 7 trout with nasal plugs intact was somewhat greater than that of 16 trout with one or both plugs missing, but not significantly so (Tables XII, XIII).

FLOAT-TRACKING STUDIES

In 1965, 37 Clear Creek and 21 Cub Creek trout and in 1966, 56 Clear Creek, 6 Cub Creek, and 24 Pelican Creek trout were float-tracked beginning at point B. Directions of "take-off" and mean vectors of trout and water current directions are shown in Figures 2 (1965) and 3 (1966). Numbers tracked, tracking times, mean directions, vector lengths, Rayleigh tests (z), and homestream tests (R) of each individual group (blind, anosmic, control, non-anesthetized) and of the groups combined for each stream each year are given in Table XV.

An eastward or east-north-eastward orientation prevailed among blind, anosmic, and control trout from Clear Creek in 1965 and 1966 and Pelican Creek in 1966. The only exception was the 1965 anosmic Clear Creek group (4 fish) whose mean direction was south-south-east. Cub Creek trout moved generally northward in 1965. However in 1966 only two trout in each category were tracked and movements were variable.

Vector lengths were usually greater for Clear and Cub Creek groups in 1965 than in 1966, with *r* values significantly greater than zero for blind, control, and combined Clear Creek trout in 1965, blind and combined Cub Creek trout in 1965, anosmic and combined Clear Creek trout in 1966, and control and combined Pelican Creek trout in 1966. Since the *r* values of the combined trout from each stream each year (except Cub Creek trout

Table XV. Tracking times, mean directions (from true North), vector lengths, Rayleigh tests, and homestream tests of blind, anosmic, control, and non-anesthetized trout from Clear, Cub, and Pelican Creeks tracked beginning at point B, 1965 and 1966. (Figures in parentheses are 95% and 99%, respectively, significant z and R values for appropriate d.f.)

Origin stream	Year	Category	Number tracked	Tracking time (min)	Mean direction (a)	Vector length (r)	Rayleigh test (z)	Homestream test (R)
Clear	1965	Blind	26	86[a] 54-162[b]	85°	0.7319	13.93** (2.97-4.48)	19.03** (11.90-13.35)
		Anosmic	4	95 55-141	152	0.4261	-[c] -	1.70 (3.20- 3.60)
		Control	37	79 51-119	66	0.4332	6.91** (2.97-4.49)	15.99** (9.20-11.65)
		Combined	67	82 51-162	79	0.5224	18.28** (2.98-4.50)	35.00** (19.20-21.40)
Cub	1965	Blind	6	74 56- 98	325	0.8234	4.07* (2.86-4.08)	4.94 (5.45- 5.65)
		Control	5	64 51- 77	354	0.9615	-[c] -	4.81** (4.35- 4.65)
		Non-anesthetized	10	85 62-120	17	0.3562	1.27 (2.92-4.29)	3.56 (4.60- 5.90)
		Combined	21	77 51-120	0	0.4696	4.63** (2.96-4.46)	9.86* (8.60-10.25)
Clear	1966	Blind	19	69 53-112	81	0.1919	0.70 (2.96-4.44)	3.65 (6.25- 8.05)
		Anosmic	19	76 57-104	49	0.4070	3.15* (2.96-4.44)	7.73* (6.15- 7.90)
		Control	18	75 54- 94	97	0.2853	1.47 (2.95-4.43)	5.14 (6.85- 8.40)
		Combined	56	73 53-112	67	0.2671	3.99* (2.97-4.50)	14.95** (10.35-14.10)

Table XV. Continued.

Origin stream	Year	Category	Number tracked	Tracking time (min)	Mean direction (a)	Vector length (r)	Rayleigh test (z)	Homestream test (R)
Cub	1966	Blind	2	69 56- 81	20	0.4472	-c/	-c/
		Anosmic	2	85 67-102	100	0.9799	-c/	-c/
		Control	2	78 71- 84	313	0.6157	-c/	-c/
		Combined	6	77 56-102	44	0.3262	0.62 (2.86-4.08)	1.96 (3.45- 4.45)
Pelican	1966	Blind	8	80 72- 89	92	0.5722	2.62 (2.90-4.20)	4.58 (4.75- 5.60)
		Anosmic	8	74 56- 96	59	0.5197	2.16 (2.90-4.20)	4.16* (3.95- 5.10)
		Control	8	67 47- 94	64	0.7174	4.12* (2.90-4.20)	5.74* (4.10- 5.20)
		Combined	24	74 47- 96	71	0.5847	8.21** (2.96-4.48)	14.03** (7.80- 9.75)
Grand Total			174	77 47-162	66	0.3958	27.25** (2.99-4.60)	

a/ Mean.
b/ Range.
c/ Sample too small for test.
* Significant at 95% level.
** Significant at 99% level.

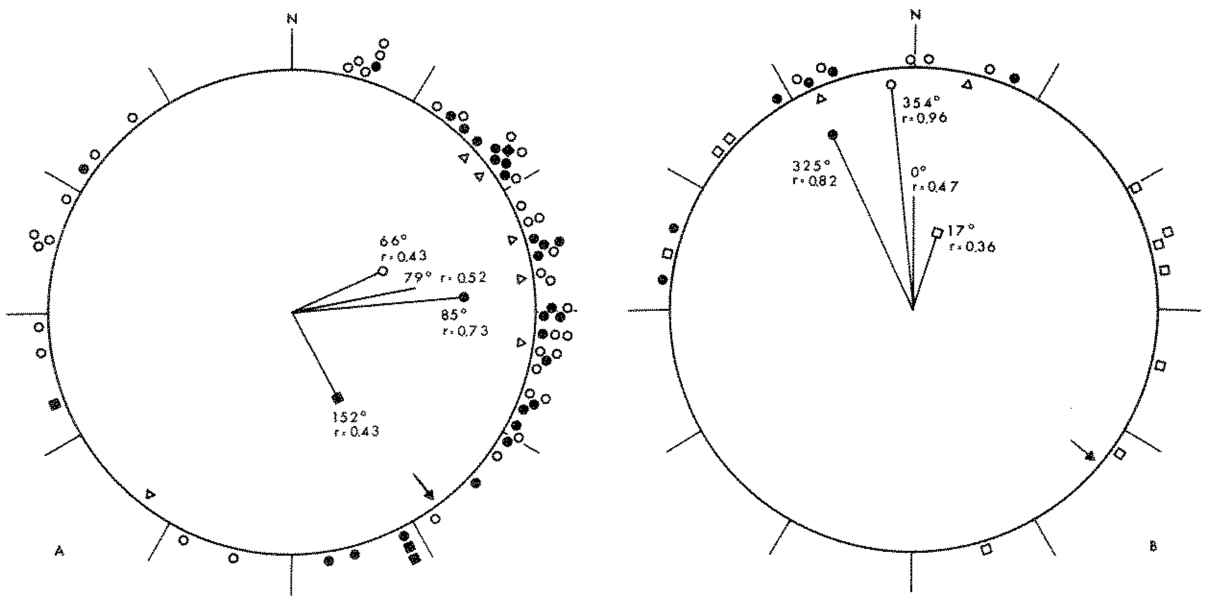

Figure 2. Directions of "take-off" (plotted in 2^{o} intervals on odd numbered degrees), mean directions, and vector lengths of (A) blind, anosmic, and control Clear Creek trout, and (B) blind, control, and non-anesthetized Cub Creek trout tracked at point B, 10-29 July, 1965. (Closed circles = blind trout, closed squares = anosmic trout, open circles = control trout, open squares = non-anesthetized trout, open triangles = 1 m current drogue. Arrow points toward homestream. Mean vectors of each group identified by appropriate symbol at end of vector. Vector without symbol is combined mean vector.)

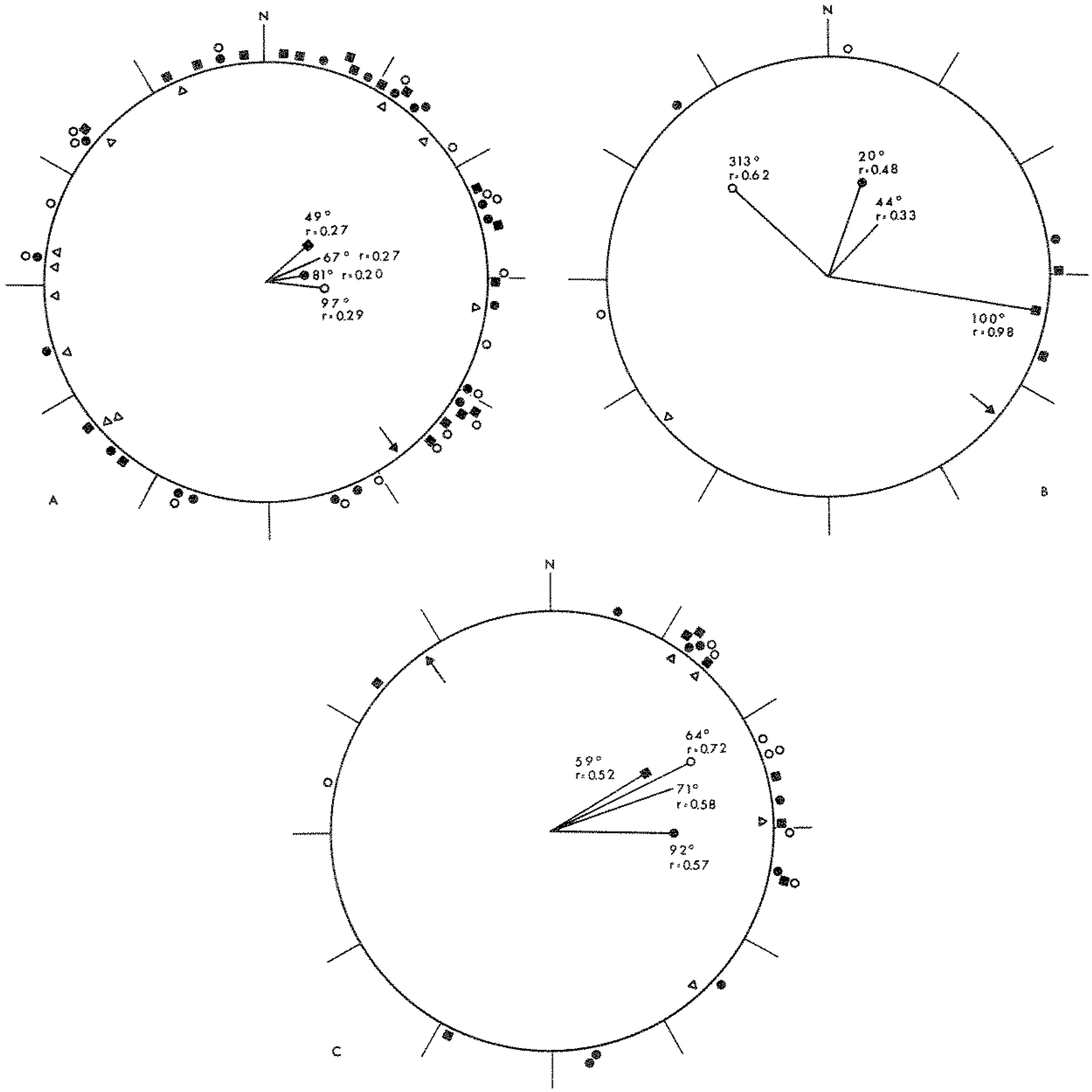

Figure 3. Directions of "take-off" (plotted in 2° intervals on odd numbered degrees), mean directions, and vector lengths of blind, anosmic, and control (A) Clear Creek trout, (B) Cub Creek trout, and (C) Pelican Creek trout tracked at point B, 2 June-18 July, 1966. (Legend as in Figure 2.)

in 1966) were significantly greater than zero, the non-significance of individual groups may be due to small sample sizes rather than lack of orientation. Pelican Creek trout *r* values were similar to 1965 Clear Creek trout *r* values.

Vector lengths, *r*, ranged from 0.1919 to 0.9799. Differences among groups from any one stream showed no pattern. Blind and anosmic trout oriented at least as well as control trout.

The orientation directions were not the same as the homestream directions for Clear, Cub, or Pelican Creek trout, and were significantly different (R test) from the homestream directions for the following groups: blind, control, and combined Clear Creek trout in 1965; blind and combined Cub Creek trout in 1965; anosmic and combined Clear Creek trout in 1966; and anosmic, control, and combined Pelican Creek trout in 1966. The non-significant differences were probably due to small sample sizes.

Resultant vector F tests were used to compare mean directions of various groups from a common stream, from different streams, and from different years (Table XVI). No mean directions of these groups within a stream for one year were significantly different, except blind and non-anesthetized trout from Cub Creek in 1965. The north orientation of Cub Creek trout in 1965 was significantly different from the east-north-east orientation of Clear Creek trout in 1965, but the differences in mean directions of all other pairs of means between streams within a group and year were not significant. The mean directions of Clear and Cub Creek trout in 1965 were not significantly different from those of 1966.

Within a given group of trout the *r* values were usually quite similar

Table XVI. F test comparisons of mean directions of float-tracked trout between various groups within streams, between streams, and between years.

Origin stream	Year	Category	v.	Origin stream	Year	Category	Directions test (F)	Significance values 95%	Significance values 99%
Clear	1965	Blind		Clear	1965	Control	1.04	4.00	7.07
		Anosmic				Control	2.51	4.09	7.33
		Anosmic				Blind	2.96	4.20	7.64
Cub	1965	Blind		Cub	1965	Control	2.22	4.84	9.65
		Blind				Non-anesthetized	6.33*	4.60	8.86
		Control				Non-anesthetized	3.68	4.67	9.07
Clear	1966	Blind		Clear	1966	Control	<1	4.13	7.44
		Anosmic				Control	2.07	4.13	7.44
		Anosmic				Blind	<1	4.13	7.44
Cub	1966	Blind		Cub	1966	Control	<1	18.51	98.50
		Anosmic				Control	5.04	18.51	98.50
		Anosmic				Blind	1.09	18.51	98.50
Pelican	1966	Blind		Pelican	1966	Control	<1	4.60	8.86
		Anosmic				Control	<1	4.60	8.86
		Anosmic				Blind	<1	4.60	8.86
Clear	1965	Blind		Cub	1965	Blind	25.71**	4.17	7.56
		Control				Control	5.21*	4.08	7.31
		Combined[a/]				Combined[b/]	13.40**	3.97	6.98
Clear	1966	Blind		Cub	1966	Blind	<1	4.38	8.18
		Anosmic				Anosmic	1.29	4.38	8.18
		Control				Control	2.86	4.41	8.29
		Combined				Combined	<1	4.00	7.08

Table XVI. Continued.

Origin stream	Year	Category	v.	Origin stream	Year	Category	Directions test (F)	Significance values 95%	Significance values 99%
Clear	1966	Blind		Pelican	1966	Blind	<1	4.24	7.77
		Anosmic				Anosmic	<1	4.24	7.77
		Control				Control	<1	4.24	7.77
		Combined				Combined	<1	3.98	7.01
Pelican	1966	Blind		Cub	1966	Blind	1.05	5.32	11.26
		Anosmic				Anosmic	<1	5.32	11.26
		Control				Control	4.08	5.32	11.26
		Combined				Combined	<1	4.20	7.64
Clear	1965	Blind		Clear	1966	Blind	<1	4.07	7.28
		Anosmic				Anosmic	3.30	4.32	8.02
		Control				Control	<1	4.03	7.20
		Combined				Combined	<1	3.92	6.85
Cub	1965	Blind		Cub	1966	Blind	<1	5.99	13.75
		Control				Control	1.25	6.61	16.26
		Combined[b/]				Combined[a/]	<1	4.24	7.77

a/ Includes anosmic trout.
b/ Includes non-anesthetized trout.
* Significant at 95% level.
** Significant at 99% level.

for males and females, and the directions of orientation of males and females were in no case significantly different (Table XVII).

Since the water current directions during the float-tracking experiments were clustered (Figures 2 and 3), the following analysis was done to determine if trout orientation was related to drift with the current or movement at some constant angle to the current. The current direction (in degrees from true North) during each track was subtracted from the direction (in degrees from true North) of each fish in that track. These converted data were then used to calculate the mean directions and vector lengths based on current direction as the zero direction. The actual mean vectors, converted mean vectors, and current mean vectors are given in Table XVIII. In general converted *r* values were equal to or smaller than unconverted values, but if the trout oriented at a constant angle to the current direction, converted *r* values would have been greater. Converted angles were in general no more clustered than unconverted angles, but would have been if the trout oriented to the current. The fact that converted *r* values and *a* concentrations remained about the same showed that the currents were clustered and not that the trout oriented to the current. In addition Clear Creek trout in 1966 showed the same east-north-east orientation, but not as strongly, when the currents were clustered to the west instead of the east (Figures 2 and 3). However in 1965 Cub Creek trout oriented toward the north, and the currents moved northward. Trout moved much farther than the current drogue drifted during the tracking period.

Since most of the float-tracking was done during the morning, the

Table XVII. Mean directions, vector lengths, and directions test comparisons of male and female trout float-tracked at point B, 1965 and 1966.

Origin stream	Year	Category	Sex	Number tracked	Mean direction (a)	Vector length (r)	Directions test (F)	Significance values 95%	Significance values 99%
Clear	1965	Blind	♂	3	61°	0.7940	<1	4.38	8.18
			♀	18	82	0.8152			
		Control	♂	8	46	0.5221	<1	4.38	8.18
			♀	13	85	0.4066			
		Combined	♂	11	51	0.5907	3.52	4.08	7.31
			♀	31	95	0.6404			
Clear	1966	Blind	♂	9	336	0.1423	2.27	4.45	8.40
			♀	10	98	0.4173			
		Anosmic	♂	8	56	0.3678	<1	4.54	8.68
			♀	9	12	0.4870			
		Control	♂	8	121	0.4803	1.40	4.54	8.68
			♀	9	60	0.3487			
		Combined	♂	25	81	0.2113	<1	4.04	7.20
			♀	28	56	0.3349			
Pelican	1966	Blind	♂	1	101	1.0000	1.96	18.51	98.50
			♀	3	46	0.8879			
		Anosmic	♂	2	98	0.7431	2.23	18.51	98.50
			♀	4	94	0.5456			
		Control	♂	3	70	0.9125	<1	5.99	13.75
			♀	5	58	0.6075			
		Combined	♂	6	57	0.6683	<1	4.49	8.53
			♀	12	63	0.6193			

Table XVIII. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and current direction (corrected) as the zero direction.

Origin stream	Year	Category	Number tracked	Uncorrected Mean direction (a)	Uncorrected Vector length (r)	Corrected Mean direction (a)	Corrected Vector length (r)
Clear	1965	Blind	18	88°	0.7044	3°	0.5231
		Control	21	79	0.2192	34	0.3326
		Combined	39	85	0.4422	16	0.4054
		Current drogue	6	59	0.7547		
Cub	1965	Blind	6	325	0.8234	327	0.8342
		Control	5	354	0.9615	357	0.9180
		Combined	11	339	0.8585	344	0.8286
		Current drogue	2	355	0.9483		
Clear	1966	Blind	19	81	0.1919	26	0.0317
		Anosmic	19	49	0.4070	65	0.4021
		Control	18	97	0.2853	194	0.2163
		Combined	56	67	0.2671	90	0.1115
		Current drogue	11	289	0.4089		
Pelican	1966	Blind	8	92	0.5722	20	0.5382
		Anosmic	8	59	0.5197	330	0.5358
		Control	8	64	0.7174	336	0.5303
		Combined	24	71	0.5847	349	0.4987
		Current drogue	4	74	0.7607		

sun azimuths during the experiments were highly clustered. The average sun azimuth during the time at large of each trout was subtracted from the direction from point B to the trout. Mean vectors were calculated from these converted data for comparison with unconverted data (Table XIX). Converted vector lengths were usually the same or slightly smaller than unconverted vector lengths, and converted angles were no more clustered than unconverted angles. Thus the trout probably did not orient at a constant angle to the sun azimuth. No tracks were made when the sun was completely obscured.

At the termination of each float-tracking experiment in 1966 most of the trout were tagged and released near point B. Recaptures of float-tracked trout from Clear and Cub Creek (Table XX) were slightly lower than those of tagged displaced trout from Clear and Cub Creek in 1966 (Table I). The low recapture of Pelican Creek trout was probably due to the damaged Pelican Creek trap. A comparison of the mean directions and vector lengths of Clear Creek trout which were float-tracked and subsequently homed with those that were not recaptured is given in Table XXI. The $\underline{r}$ values of the home group were higher than those of the non-return group for blind, anosmic, and combined groups, but not for controls. In general sample sizes were too small for statistical significance of $\underline{r}$ values or homestream tests. The mean directions of home and non-return groups were not significantly different.

Three long-time float-tracks for Clear Creek trout beginning at point B are plotted in Figure 4. A control trout (No. 1 - ripe female) was tracked 6 hr 20 min on 31 July 1965 during which time she traveled

Table XIX. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and sun azimuth (corrected) as the zero direction.

Origin stream	Year	Category	Number tracked	Uncorrected Mean direction (a)	Uncorrected Vector length (r)	Corrected Mean direction (a)	Corrected Vector length (r)
Clear	1965	Blind	26	85°	0.7319	327°	0.6212
		Anosmic	4	152	0.4261	48	0.4266
		Control	37	66	0.4322	294	0.4474
		Combined	67	79	0.5224	313	0.4665
		Sun azimuth	67	115	0.8896		
Cub	1965	Blind	6	325	0.8234	181	0.7929
		Control	5	354	0.9615	222	0.8423
		Non-anesthetized	10	17	0.3562	306	0.3726
		Combined	21	0	0.4696	226	0.3926
		Sun azimuth	21	130	0.9266		
Clear	1966	Blind	19	81	0.1919	341	0.2370
		Anosmic	18	97	0.2853	351	0.3208
		Control	19	49	0.4070	294	0.3253
		Combined	56	67	0.2671	327	0.2654
		Sun azimuth	56	105	0.9443		
Pelican	1966	Blind	8	92	0.5722	1	0.5523
		Anosmic	8	64	0.7174	328	0.5286
		Control	8	59	0.5197	334	0.7056
		Combined	24	71	0.5847	340	0.5785
		Sun azimuth	24	92	0.9978		

Table XX. Recapture of Clear, Cub, and Pelican Creek trout tagged and released following float-tracking at point B, 1966. (Percentages in parentheses.)

Origin stream	Category	Number released	Number of recaptures Homing	Straying	Angling	Total
Clear	Blind	18	8(44.4)	1(5.6)	0(0.0)	9(50.0)
	Anosmic	18	2(11.1)	0(0.0)	1(5.6)	3(16.7)
	Control	18	10(55.6)	0(0.0)	0(0.0)	10(55.6)
	Total	54	20(37.0)	1(1.9)	1(1.9)	22(40.8)
Cub	Blind	2	2(100.0)	0(0.0)	0(0.0)	2(100.0)
	Anosmic	2	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Control	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Total	5	2(40.0)	0(0.0)	0(0.0)	2(40.0)
Pelican	Blind	7	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Anosmic	7	1(14.3)	0(0.0)	0(0.0)	1(14.3)
	Control	8	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Total	22	1(4.5)	0(0.0)	0(0.0)	1(4.5)

6.2 km (average speed 1.0 km/hr) ending about 60% of the distance from point B to Clear Creek. A blind trout (No. 2 - ripe female) was tracked 3 hr 26 min on 1 August 1965 during which time she traveled 2.1 km (0.6 km/hr) in a southwesterly direction. The weather was clear and sunny during both these tracks. A non-anesthetized trout (No. 3 - ripe male) was tracked 3 hr 56 min on 31 May 1966 during which time he traveled 3.1 km (0.8 km/hr), first northward, then eastward to the vicinity of a small island, and then westward. The weather was initially clear, changing to cloudy with light rain while the trout was near the island, and then clearing for the remainder of the time. This trout was tagged at the end of the tracking period and was recaptured in the homestream 11 days later.

ANGLER RETURNS

Twenty tags from Clear Creek trout and 13 from Cub Creek trout were

Table XXI. Comparison of mean directions and vector lengths of Clear Creek trout recaptured in the homestream with those not recaptured following float-tracking at point B, 1966. (Figures in parentheses are 95% and 99%, respectively, z, R, and F values for appropriate d.f.)

Category	Number tracked	Mean direction (a)	Vector length (r)	Rayleigh test (z)	Homestream test (R)	Directions test (F)
Blind Home	8	113°	0.4502	1.62 (2.90-4.20)	3.60 (4.85- 5.75)	1.46 (4.54-8.68)
Non-return	9	22	0.1592	0.23 (2.91-4.25)	1.43 (4.25- 5.45)	
Anosmic Home	2	13	0.9903	- a/	- a/	<1 (4.60-8.86)
Non-return	14	25	0.3714	1.93 (2.94-4.29)	5.20 (5.85- 7.15)	
Control Home	10	62	0.4456	1.99 (2.92-4.29)	4.46 (4.50- 5.78)	3.53 (4.54-8.68)
Non-return	7	146	0.5333	1.99 (2.88-4.16)	3.73 (5.10- 5.70)	
Combined Home	20	19	0.4068	3.31* (2.96-4.45)	8.14* (7.60- 9.20)	<1 (4.04-7.19)
Non-return	30	31	0.1892	1.07 (2.97-4.49)	5.68 (7.90-10.10)	

a/ Sample too small for test.
* Significant at 95% level.

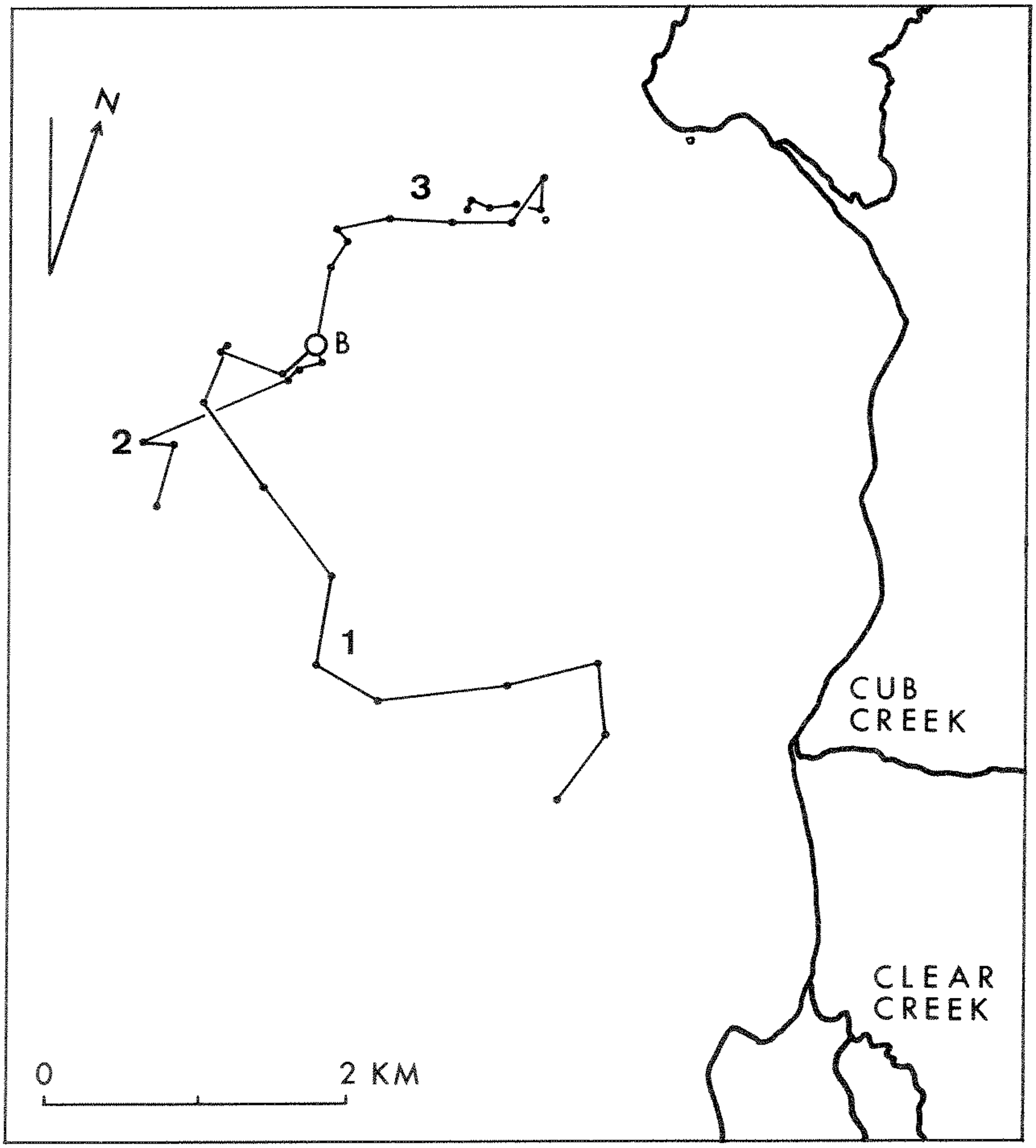

Figure 4. Float-tracks of three Clear Creek trout beginning at point B: 1. Control trout, 31 July 1965, 6 hr 20 min; 2. Blind trout, 1 August 1965, 3 hr 26 min; 3. Non-anesthetized trout, 31 May 1966, 3 hr 56 min.

returned by anglers. These trout had been released at points A, B, C, D, and E (Figure 1). In general the distribution of angler recaptures reflected fishing pressure which was concentrated along the western, northern, and northeastern shores. Distribution of angler recaptures was as follows:

Recapture area in lake	Number of returns	Distances traveled (km)
Western portion	9	7.4-23.5
Northwestern portion	6	4.6-10.4
Outlet, Yellowstone River	3	7.8-10.4
Northeastern portion	9	2.0-5.2
Near Cub Creek	3	1.3-3.9
Near Clear Creek	3	0.2-7.7

Two trout homed prior to angling recapture. Times from release to recapture ranged from 0.5-45 days within one season, and two opercle-tagged trout were recaptured just over one year after release. In general opercle-tagged trout were at large longer (2.5-46 days) than those tagged with alligator clips (0.5-16.5 days). Recaptures were distributed widely in the heavily fished areas of the lake and were not clustered near the release points or the homestreams. No trout were recaptured in the southern portion of the lake, but fishing pressure there was extremely light.

DISCUSSION

Homing percentages and total recapture percentages of both Clear and Cub Creek trout were strikingly lower, and homing time was much less in 1964 than in 1965 and 1966. Either the handling procedure or the lateness in the spawning season when the experiments were conducted in 1964 or both were believed responsible. For opercle tagging in 1964 the trout had to be anesthetized and total time from netting to release was as much as 2 hr — three times longer than for alligator clip tagging in 1965 and 1966. Comparison of control and non-anesthetized trout in 1966 showed that anesthetic as such did not affect homing percentages or times. Black and Connor (1964) found that anesthetization of rainbow trout (with MS 222) did not change blood lactate or muscle glycogen, but Black and Barrett (1957) reported that even minimal handling and transportation for a 2 hr period caused significant increases in muscular activity and blood lactate in cutthroat and steelhead trout. Parker et al. (1963) emphasized any time taken to obtain a measurement may contribute significantly to fatigue.

The opercle tag may have contributed to mortality or aberrant behavior. Mechanical abrasion of the underlying gill tissue was apparent in most recaptured cutthroat trout with opercle tags. Rectangular sections of the posterior edge of the operculum were missing from many recaptured trout indicating that tag loss may have been significant. Marlborough (1963) reported opercle tag abrasion and loss in *Cyprinus carpio* and *Carassius carassius*. Miller (1957) stated that cutthroat trout behavior was affected by Petersen tags, and Clancy (1963) showed that swimming endurance of steelhead fingerlings tagged with Petersen tags was permanently reduced about half. On the other hand Gunning (1965) reported that movement behavior in streams of longear sunfish (*Lepomis megalotis*) was not affected by opercle tags.

Greater loss of opercle tags than alligator clips would contribute to an apparent lower return and faster homing time, since the slower trout would have more time to lose tags. No comparative tag loss information is available however.

In 1964 abnormally high run-off prevented adequate displacement experiments until after the peak of the spawning run had occurred. Toward the end of the spawning season trout may have had less motivation to spawn. The delay caused by displacement may have allowed environmental conditions to develop which were not conducive to cutthroat trout migration and spawning. This would also result in an apparent faster return time of those recaptured. In 1966 a control group and a non-anesthetized group released about a week later than two similar groups had an average homing time only half as long. Thus homing times showed a real or apparent decrease as the migration season progressed.

The average homing times reported here are much slower than the fastest times. The fastest homing speeds, which were 19 cm/sec (0.7 km/hr), were recorded for Clear Creek trout released at point B. In terms of trout length these speeds ranged from 0.50-0.65 lengths (L)/sec. They are similar to those exhibited by three trout float-tracked for several hours (0.4-0.7 L/sec), and to the average speeds of Clear and Cub Creek trout (0.59 L/sec and 0.48 L/sec, respectively) float-tracked for 1 hr from a mid-lake point by Jahn (1966). These speeds are somewhat lower than the 0.9-1.7 L/sec for sockeye and coho salmon in actual up-river migration (Ellis 1966). All of the above values are well below sustained swimming speeds obtained in the laboratory for sockeye salmon (3.0 L/sec) by Brett (1965) and trout (*Salmo irideus*) (2.0 L/sec) by Bainbridge (1962). However, in the case of cutthroat trout a straight line journey is assumed for homing individuals so the distance estimate is minimal. Trout may have entered the trap some time before being recorded so the time estimate is maximal. The tracked trout were towing the Styrofoam floats which probably reduced swimming speed.

Trout homed from just outside the stream mouth at about the same or even slower speed than those from much greater distances. The displacement of migrating trout may cause physiological and behavioral changes resulting in delay while the trout begins a new sequence of events leading to migration and spawning. This delay may occur near the mouth of the stream where salmonids are known to congregate prior to upstream migration. The three long-time float-tracks showed that trout can make fairly rapid and direct progress even while towing a float. The actual path and timing of homing travel needs further investigation.

The amount of straying exchange for trout between Cub and Clear Creek during the in-season displacement experiments is higher than that reported by Cope (1957) for repeat homing experiments. Of his recaptures 3.3% strayed, as contrasted to 14.3% in the present study, and 0.0% during the natal homing studies of Ball (1955). During the experiments of Cope and Ball five and six streams, respectively, had fish traps, while in the present study only Clear and Cub Creeks had effective traps. Natal and repeat homing provide the genetic separation necessary to produce and maintain subpopulations of cutthroat trout in the Yellowstone Lake drainage reported by Cope (1957) and Bulkley (1963). Straying of first-time and repeat spawners prevents complete isolation of the various spawning runs. The distribution of angler recaptures supports the generally accepted conclusion that the subpopulations of trout in Yellowstone Lake are not spatially segregated except during the spawning period when the trout have ascended the tributaries. In-season homing and straying would not affect spawning season segregation of subpopulations, since in-season displacement is not a part of the cutthroat life history. Some portion of the straying may be an artifact due to so-called "proving" suggested by Ricker (MS 1959) in which a fish may ascend a "wrong" tributary some distance and then reject it. However if a trap is across the stream, the fish is caught and recorded as a stray. This may well occur in Clear and Cub Creek, since the traps are quite close to the stream mouths.

The east-north-eastward orientation of Clear Creek trout and the northward orientation of Cub Creek trout at point B in the present study were quite similar to the northeastward and northward orientation of Clear and Cub Creek trout, respectively, tracked from a mid-lake point by Jahn (1966). This was true even though the directions to Clear and Cub Creeks from point B are 130° and 143°, respectively, and from the mid-lake point are 73° and 93°, respectively. The orientation of Pelican Creek trout was also east-north-eastward, but Pelican Creek is 325° from point B. Clear and Cub Creek trout tracked as long as 2 hr by Jahn (1966) from a point near the Clear and Cub Creek shore went generally eastward (shoreward).

Apparently this orientation is a compass (Type II) rather than a navigation or goal finding (Type III), since the direction of orientation was the same at different release points and was not in the direction of the homestream. Moreover Clear and Pelican Creek trout oriented in the same direction even though their homestreams were in opposite directions. Perhaps an eastward or northward orientation is a feature of other spawning populations of cutthroat trout in Yellowstone Lake, however no trout from streams on the west side of the lake have been tracked. The ability to maintain a constant compass direction until shore or bottom is available for cues and then paralleling the shoreline would be a considerable improvement over random search in homing from open-water points in Yellowstone Lake.

The possibility exists that non-spawning trout may also have an orientation. White bass displaced from spawning areas and tracked from a mid-lake point in Lake Mendota, Wisconsin, showed a marked orientation toward their homespawning ground (Hasler et al. 1965, Gardella MS 1967), but non-spawners tracked from the same point also showed a strong orientation in the same direction (Gardella MS 1967).

Blind, anosmic, control, and non-anesthetized cutthroat trout showed similar orientation. Blind and anosmic trout were able to home as well as the control and non-anesthetized trout, but slower in the case of the blind trout. Jahn (1966) for cutthroat trout, Hasler et al. (1958) for white bass, and Winn et al. (1964) for parrot fishes have all presented evidence for partial or complete loss of orientation under overcast skies. However blind cutthroat trout were not disoriented. Groot (1965) showed that seaward migrating sockeye salmon smolts possess more than one orientation mechanism. Under clear skies a celestial orientation (sun and polarized light) was used, and as clouds built up the dispersion of the orientation increased. Under complete overcast, however, orientation was again exhibited, and was attributed by Groot to non-celestial phenomena (X-orientation). In addition landmark orientation occurred. Winn et al. (1964) believed the sun and not the polarization pattern to be responsible for the orientation of parrot fishes. Cutthroat trout may orient at night, since Pacific salmon are known to do so (Brett and Groot 1963).

Results obtained in this study and that of Jahn (1966) suggest that celestial cues may be used by cutthroat trout for orientation if available, but other orientation mechanisms may be used if vision of celestial cues is prevented. Tracking of trout at night and of trout whose internal clocks had been shifted would provide important information on celestial orientation.

Olfactory occlusion prevented migrating silver salmon from making the proper choice at a stream fork (Wisby and Hasler 1954), but olfactory occlusion apparently did not prevent cutthroat trout from choosing the proper stream in Yellowstone Lake. The displacement of anosmic trout should be repeated with an improved occlusion technique to provide conclusive results. Anosmic trout that were float-tracked oriented as well as controls which is in keeping with the hypothesis that odor could not play a directing role in orientation in large bodies of water (Hasler 1966, Brett and Groot 1963).

ACKNOWLEDGEMENTS

Thanks are due Dr C. J. D. Brown, who directed the study and assisted in preparation of the manuscript, and to Dr R. M. Horrall and Messrs L. A. Jahn and Q. J. Stober, who gave many suggestions and help in the field. To my wife, Barbara, go special thanks for her continual encouragement and her tolerance of my absence while working in the field. Excellent cooperation was received from the National Park Service and Mr F. P. Sharpe and his crew of the U. S. Fish and Wildlife Service. Dr W. H. Sippel generously loaned a boat and house trailer for use in this study. Funds and equipment for the first year of the study were provided by the Cooperative Fisheries Unit at Montana State University, the Department of Zoology and Entomology, Federal Water Pollution Control Administration Training Grant No. 1T1-WP-1 administered by Dr J. C. Wright, and by the Yellowstone Library and Museum Association through Mr J. M. Good. Funds for the second and third years of the study were supplied by grants from the National Science Foundation (grant #GB-3512) and the Office of Naval Research (grant #NR 301-854, contract nonr 4840) awarded to Dr C. J. D. Brown.

LITERATURE CITED

Adler, H. E. 1963. Sensory factors in migration. Anim. Behav. 11(4): 566-577.

Armstrong, R. H. 1965. Some migratory habits of the anadromous Dolly Varden *Salvelinus malma* (Walbaum) in Southeastern Alaska. Alaska Dep. Fish and Game, Res. Rep. 3:1-36.

Bainbridge, R. 1962. Training, speed and stamina in trout. J. Exp. Biol. 39:537-555.

Ball, O. P. 1955. Some aspects of homing in cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett. 32:75-80.

Ball, O. P., and O. B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U. S. Fish and Wildl. Ser., Res. Rep. 55:1-62.

Bardach, J. E., and J. Case. 1965. Sensory capabilities of the modified fins of squirrel hake (Urophycis chuss) and searobins (Prionotus carolinus and P. evolans). Copeia 1965(2):194-206.

Barlow, J. S. 1964. Inertial navigation as a basis for animal navigation. J. Theoret. Biol. 6:76-117.

Bartlett, M. S. 1937a. Properties of sufficiency and statistical tests. Proc. Roy. Soc. A160:268-282.

____________. 1937b. Some examples of statistical methods of research in agriculture and applied biology. J. Roy. Stat. Soc. Suppl. 4: 137-183.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Amer. Inst. Biol. Sci. Washington. 57pp.

Benson, N. G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U. S. Fish and Wildl. Ser., Res. Rep. 56:1-33.

Black, E. C., and I. Barrett. 1957. Increase in levels of lactic acid in the blood of cutthroat and steelhead trout following handling and live transportation. Can. Fish Cult. 20:13-24.

Black, E. C., and A. R. Conner. 1964. Effects of MS 222 on glycogen and lactate levels in rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Canada 21(6): 1539-1542.

Braemer, W. 1960. A critical review of the sun-azimuth hypothesis. Cold Spring Harbor Symp. 25:413-427.

Braemer, W., and H. O. Schwassmann. 1963. Vom Rhythmus der Sonnenorientierung am Äquator (bei Fischen). Ergebn. Biol. 26:182-201.

Brett, J. R. 1965. The relation of size to rate of oxygen comsumption and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada 22(6):1491-1501.

Brett, J. R., and C. Groot. 1963. Some aspects of olfactory and visual responses in Pacific salmon. J. Fish. Res. Bd. Canada 20(2):287-303.

Bulkley, R. V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U. S. Fish and Wildl. Ser., Res. Rep. 54:1-31.

Bulkley, R. V. 1963. Natural variation in spotting, hyoid teeth counts, and coloration of Yellowstone cutthroat trout, Salmo clarki lewisi Girard. U. S. Fish and Wildl. Ser., Spec. Sci. Rep. — Fish. 460: 1-11.

Clancy, D. W. 1963. Effect of tagging with Petersen disc tags on the swimming ability of fingerling steelhead trout (Salmo gairdneri). J. Fish. Res. Bd. Canada 20(4):969-981.

Clemens, W. A., R. E. Foerster, and A. L. Pritchard. 1939. The migration of Pacific salmon in British Columbia waters. In: The migration and conservation of salmon. Amer. Ass. Advance. Sci., Publ. 8:51-59.

Cope, O. B. 1957. Races of cutthroat trout in Yellowstone Lake. U. S. Fish and Wildl. Ser., Spec. Sci. Rep. 208:74-84.

Donaldson, L. R., and G. H. Allen. 1957. Return of silver salmon, Oncorhynchus kisutch (Walbaum) to point of release. Trans. Amer. Fish. Soc. 87:13-22.

Duncan, D. B. 1955. Multiple range and multiple F tests. Biometrics 11:1-42.

Ellis, D. V. 1966. Swimming speeds of sockeye and coho salmon on spawning migration. J. Fish. Res. Bd. Canada 23(2):181-187.

Eschmeyer, P. H. 1954. The reproduction of lake trout in southern Lake Superior. Trans. Amer. Fish. Soc. 84:47-74.

Fagerlund, U. H. M., J. R. McBride, M. Smith, and N. Tomlinson. 1963. Olfactory perception in migrating salmon. III. Stimulants for adult sockeye salmon (Oncorhynchus nerka) in home stream waters. J. Fish. Res. Bd. Canada 20(6):1457-1463.

Frost, W. E. 1963. The homing of charr Salvelinus willughbii (Günther) in Windermere. Anim. Behav. 11(1): 74-82.

Gardella, E. S. 1967. The study of open-water orientation of white bass, Roccus chrysops (Rafinesque), by the use of ultrasonic tracking methods. M.S. Thesis. Univ. Wis. 62pp.

Gerking, S. D. 1959. The restricted movement of fish populations. Biol. Rev. 34:221-242.

____________. 1964. Home range of lake fishes. Indiana Aquatic Res. Unit Rep. 36pp. Mimeo.

Greenwood, J. A., and D. Durand. 1955. The distribution of length and components of the sum of n random unit vectors. Ann. Math. Stat. 26:233-246.

Griffin, D. R. 1952. Bird Navigation. Biol. Rev. 27:359-393.

Groot, C. 1965. On the orientation of young sockeye salmon (Oncorhynchus nerka) during their seaward migration out of lakes. Behavior, Suppl. 14:1-198.

Gunning, G. E. 1965. A behavioral analysis of the movement of tagged longear sunfish. Prog. Fish-Cult. 27(4):211-215.

Hara, T. J., K. Ueda, and A. Gorbman. 1965. Electroencephalographic studies of homing salmon. Science 149(3686):884-885.

Hartman, W. L., and R. F. Raleigh. 1964. Tributary homing of sockeye salmon at Brooks and Karluk Lakes, Alaska. J. Fish Res. Bd. Canada 21(3):485-504.

Hasler, A. D. 1956a. Influence of environmental reference points on learned orientation in fish (Phoxinus). Z. vergl. Physiol. 38: 303-310.

____________. 1956b. Perception of pathways by fishes in migration. Quart. Rev. Biol. 31(3):200-209.

____________. 1960a. Homing orientation in migrating fishes. Ergebn. Biol. 23:94-115.

____________. 1960b. Guideposts of migrating fishes. Science 132 (3430):785-792.

____________. 1966. Underwater guideposts. Univ. Wis. Press. Madison. 155pp.

Hasler, A. D., H. F. Henderson, R. M. Horrall, and E. S. Gardella. 1965. Orientation of homing white bass. Amer. Zool. 5(4):383. (Abstr. only.)

Hasler, A. D., R. M. Horrall, W. J. Wisby, and W. Braemer. 1958. Sun-orientation and homing in fishes. Limnol. Oceanogr. 3(4):353-361.

Hasler, A. D., and H. O. Schwassmann. 1960. Sun orientation of fish at different latitudes. Cold Spring Harbor Symp. 25:429-441.

Hasler, A. D., and W. J. Wisby. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Amer. Natur. 85(823):223-238.

________________________. 1958. The return of displaced large-mouth bass and green sunfish to a "home" area. Ecology 39(2):289-293.

Helle, J. H. 1966. Behavior of displaced adult pink salmon. Trans. Amer. Fish. Soc. 95(2):188-195.

Henderson, H. F. 1963. Orientation of pelagic fishes: (I) Optical problems (II) Sonic tracking. Ph.D. Thesis. Univ. Wis. 135pp.

Horrall, R. M. 1961. A comparative study of two spawning populations of the white bass, Roccus chrysops (Rafinesque), in Lake Mendota, Wisconsin, with special reference to homing behavior. Ph.D. Thesis. Univ. Wis. 181pp.

Idler, D. R., J. R. McBride, R. E. E. Jonas, and N. Tomlinson. 1961. Olfactory perception in migrating salmon. II. Studies on a laboratory bio-assay for homestream water and mammalian repellent. Can. J. Biochem. Physiol. 39:1575-1584.

Jahn, L. A. 1966. Open-water movements of the cutthroat trout (Salmo clarki) in Yellowstone Lake after displacement from spawning streams. J. Fish. Res. Bd. Canada 23(10):1475-1485.

Johnson, W. E., and C. Groot. 1963. Observations on the migration of young sockeye salmon (Oncorhynchus nerka) through a large, complex lake system. J. Fish. Res. Bd. Canada 20(4):919-938.

Jones, J. W. 1959. The salmon. Harper and Bros. New York, 192pp.

Kruse, T. E. 1959. Grayling of Grebe Lake, Yellowstone National Park, Wyoming. U. S. Fish and Wildl. Ser., Fish. Bull. 59(149):307-351.

Lindsey, C. C., T. G. Northcote, and G. F. Hartman. 1959. Homing of rainbow trout to inlet and outlet spawning streams at Loon Lake, British Columbia. J. Fish. Res. Bd. Canada 16(5):695-719.

Loftus, K. H. 1957. Studies on river spawning populations of lake trout in eastern Lake Superior. Trans. Amer. Fish. Soc. 87:259-277.

Marlborough, D. 1963. The unsuitability of monel metal opercular strap tags for tagging carp. Prog. Fish-Cult. 25(3):155-158.

Martin, N. V. 1960. Homing behavior in spawning lake trout. Can. Fish Cult. 26:3-6.

McBride, J. R., U. H. M. Fagerlund, M. Smith, and N. Tomlinson. 1964. Olfactory perception in juvenile salmon. II. Conditioned response of juvenile sockeye salmon (Oncorhynchus nerka) to lake waters. Can. J. Zool. 42:245-248.

McCleave, J. D., L. A. Jahn, and C. J. D. Brown. 1967. Miniature alligator clips as fish tags. Prog. Fish-Cult. 29(1):60-61.

Miller, R. B. 1954. Movements of cutthroat trout after different periods of retention upstream and downstream from their homes. J. Fish. Res. Bd. Canada 11(5):550-558.

————————. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. J. Fish. Res. Bd. Canada 14(5):687-691.

Neave, F. 1964. Ocean migrations of Pacific salmon. J. Fish. Res. Bd. Canada 21(5):1227-1244.

Parker, R. R., E. C. Black, and P. A. Larkin. 1963. Some aspects of fish-marking mortality. Cons. Int. Explor. Mer 370:117-122.

Patten, B. C. 1964. The rational decision process in salmon migration. J. Cons. Int. Explor. Mer 28(3):410-417.

Platts, W. S. 1959. Homing, movements, and mortality of wild cutthroat trout (Salmo clarki Richardson) spawned artificially. Prog. Fish-Cult. 21(1):36-38.

Ricker, W. E. 1959. Evidence for environmental and genetic influence on certain characters which distinguish stocks of the Pacific salmons and steelhead trout. MS. 129pp.

Saila, S. B., and R. A. Shappy. 1963. Random movement and orientation in salmon migration. J. Cons. Int. Explor. Mer 28(1):153-166.

Scheer, B. T. 1939. Homing instinct in salmon. Quart. Rev. Biol. 14: 408-430.

Schwassmann, H. O. 1960. Environmental cues in the orientation rhythm of fish. Cold Spring Harbor Symp. 25:443-450.

Schwassmann, H. O., and W. Braemer. 1961. The effect of experimentally changed photoperiod on the sun-orientation rhythm of fish. Physiol. Zool. 34(4):273-286.

Schwassmann, H. O., and A. D. Hasler. 1964. The role of the sun's altitude in sun orientation of fish. Physiol. Zool. 37(2):163-178.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish and Game, Fish. Bull. 98:1-375.

Smith, M. W., and J. W. Saunders. 1958. Movements of brook trout, Salvelinus fontinalis (Mitchill), between and within fresh and salt water. J. Fish. Res. Bd. Canada 15(6):1403-1449.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill. New York. 481pp.

Stephens, M. A. 1962. Exact and approximate tests for directions. I. Biometrika 49:463-477.

Stuart, T. A. 1957. The migrations and homing behavior of brown trout (*Salmo trutta* L.). Scottish Home Dep., Freshwater and Salmon Fish. Res. 18:1-27.

Vladykov, V. D. 1942. Precision with which speckled trout (*Salvelinus fontinalis*) return to the same spawning grounds. Can. Field Natur. 56(8/9):134-136.

Watson, G. S., and E. J. Williams. 1956. On the construction of significance tests on the circle and the sphere. Biometrika 43:344-352.

White, H. C., and A. G. Huntsman. 1938. Is local behavior in salmon heritable? J. Fish. Res. Bd. Canada 4(1):1-18.

Wickett, W. P. 1958. Adult returns of pink salmon from the 1954 Fraser River planting. Fish. Res. Bd. Canada, Progr. Rep. Pac. Coast Sta. 111:18-19.

Winn, H. E., M. Salmon, and N. Roberts. 1964. Sun compass orientation by parrot fishes. Z. Tierpsychol. 21(7):798-812.

Wisby, W. J., and A. D. Hasler. 1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). J. Fish. Res. Bd. Canada 11(4):472-478.