Orientation Differences Between Populations of Juvenile Sockeye Salmon

K. S. Simpson

Department of Fisheries and the Environment
Fisheries and Marine Service
Resource Services Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6

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FISHERIES AND MARINE SERVICE

TECHNICAL REPORT 717

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Department of Fisheries and the Environment
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PREFACE

This report is the reproduction of a thesis submitted in December, 1973, to the University of Victoria (Victoria, British Columbia) in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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ABSTRACT

Simpson, K. S. 1979. Orientation differences between populations of juvenile sockeye salmon. Fish. Mar. Serv. Tech. Rep. 717: 114 p.

British Columbia's Babine Lake system has three populations of sockeye salmon smolts which travel different routes to the outlet on their seaward migration. The objective of this study was to determine if the directional preferences of these populations are innately different. Smolts from five streams which contribute to the lake populations were raised from the egg in similar conditions and their directional preferences tested.

Most individuals were strongly oriented. These preferences were diverse but not random within each stream sample. Orientation tested indoors and outdoors was strongly affected by positive and negative phototaxis and photonegativity, respectively. However, the Morrison indoors group had migratory orientation, changing preferences clockwise from south almost 360° around to southeast at a rate of 3.0° per day, in approximate correspondence to the lake route.

Observed orientations were significantly different between most samples, supporting the hypothesis that progeny from these streams are genetically distinct. The study's objective of whether the migration-adaptive orientation observed at Babine Lake has innate differences remains to be shown.

Key words: Orientation, behaviour, *Oncorhynchus nerka*, smolts, Babine Lake, migration, population characteristics, innate differences.

RÉSUMÉ

Simpson, K.S. 1979. Orientation differences between populations of Juvenile sockeye salmon. Fish. Mar. Serv. Tech. Rep. 717: 114 p.

Le bassin du lac Babine (C. - B.) renferme trois populations de smolts de sockeye qui empruntent des voies différentes pour migrer vers la mer. L'A. a voulu déterminer si cette préférence était innée. Des smolts de cinq cours d'eau, appelés à se rendre dans le lac, ont été élevés dans des conditions indentiques depuis leur incubation afin de vérifier s'ils prenaient ensuite une direction déterminée.

La plupart d'entre eux ont opté pour une direction précise. Dans chaque échantillon, ces préférences, variées, n'ont cependant pas été le fait du hasard. L'orientation, étudiée à l'intérieur et à l'extérieur, dépendait fortement d'une phototaxie positive et négative dans le premier cas et de la photonégativité dans l'autre. Par contre, le groupe Morrison situé à l'intérieur a modifié sa route en se déplacant, à raison de 3°,0 par jour vers la droite, de presque 360^{o} à partir du sud jusqu'au sud-est, de manière à suivre a peu près la route vers le lac.

Entre la plupart des échantillons, l'orientation a varié considérablement, ce qui tend à confirmer l'hypothèse selon laquelle ces cours d'eau hébergeraient des populations génétiquement distinctes.

Quant à savoir di l'orientation adaptive observée chez le saumon du lac Babine en vue de sa migration comporte des différences innées, il reste à le prouver.

Mots clefs: Orientation; comportement; *Oncorhynchus nerka*; smolts; la Babine; migration; traits distinctifs des populations; différences innées.

INTRODUCTION

Sockeye salmon (Oncorhynchus nerka) typically spawn in outlet and inlet streams of Babine Lake from September to November. The spawning streams are clustered in three regions (Fig. 1): (1) at the outlet (Upper and Lower Babine rivers), (2) near Morrison Lake, and (3) in the "Main Lake" area of southern Babine Lake (Fulton River and Pinkut Creek are the principal streams). By early spring, fry leave the gravel beds and migrate to the lake. Progeny from the three regions remain essentially separated during their lake life (Fig. 1) (Johnson 1956, 1958; McDonald 1969). Virtually all leave after 1 year, between the beginning of May and mid-June.

The seaward migration of Babine smolts is precisely timed and well directed (Johnson and Groot 1963; Groot 1965, 1972). Groot found that smolts kept in tanks preferred directions approximating those expected in their lake population's migration. Morrison smolts even changed directions during their captivity as they would if they were travelling the route (see below). His subjects probably used the sun and polarized light as orientation cues under clear skies and an unknown mechanism was used in overcast (Groot 1965). Recent sophisticated studies show that lake currents in the Main Lake basin are largely wind-driven (D. Farmer, personal communication) and too variable to be useful as a cue.

This study asks the question: What determines the direction of seaward migration in these lake populations? My hypothesis is that each population has genetically distinct directional tendencies which correspond to the routes necessary to reach the outlet. It is based on the following observations:

(1) Each lake population takes a different route to the outlet (Fig. 1). Morrison fish travel SSE through Morrison Arm and then almost reverse direction to go up the North Arm. Main Lake fish migrate NW and then N while Nilkitkwa Lake-North Arm smolts make a short northward journey.

(2) Main and Morrison lake groups make the journey for the first time.

To check this hypothesis, I raised samples from the three lake populations under identical conditions and tested the smolts for orientation differences. There are three questions related to this objective:

(1) Do sockeye smolts show directional tendencies under experimental conditions?

(2) Do samples from different lake populations reveal significantly different directional tendencies?

(3) Do the directional tendencies correspond to theoretical migration directions from nursery areas to outlet?

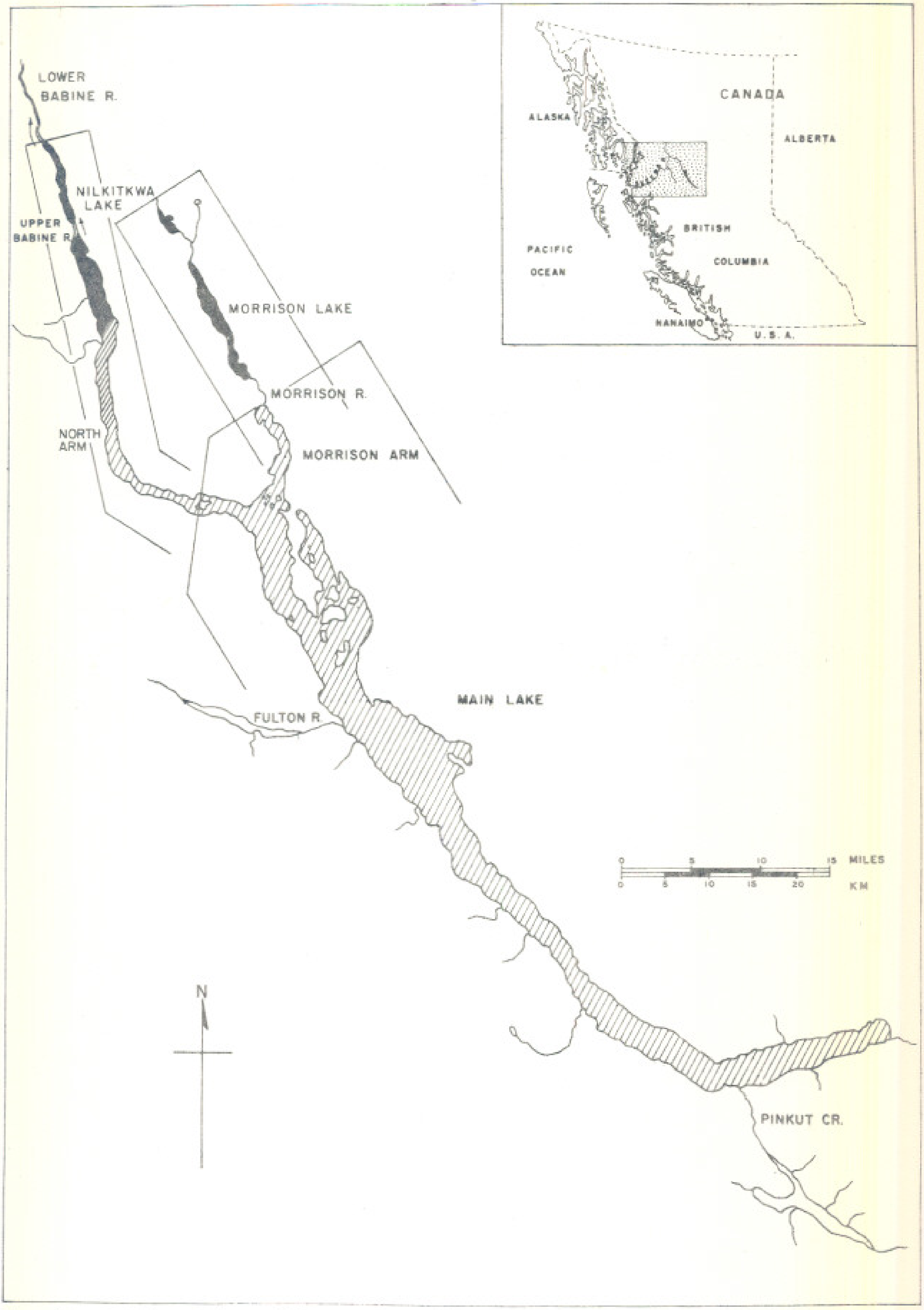

Fig. 1. Babine Lake and its main sockeye spawning streams. Shaded areas show the three lake populations of sockeye smolts before migration. The degree of shading is approximately proportional to population density. The North Arm and Morrison populations are primarily located in Nilkitkwa and Morrison lakes, respectively.

DEFINITIONS

Innate. Morphological or behavioural differences between individuals or populations not affected by the environment during ontogenetic development.

Lake population (in Babine Lake). Juvenile sockeye in one of the three nursery areas. Each population contains several genetically semi-isolated river stocks.

Directional preference. The mean direction taken by an animal when the distribution of directions is significantly different from uniform.

Orientation. " . . . a selective process in which certain stimuli in the environment illicit a response sequence that results in a non-random pattern of locomotion, direction of the body axis, or both." (Adler 1970).

Phototaxis. Directed orientation reaction towards or away from a light stimulus (Fraenkel and Gunn 1961).

MATERIALS AND METHODS

I ran experiments in April, May, and June of 1970 and 1971 (Table 1). The main text only deals with the 1971 experiments. The 1970 methods and results are in Appendix A (p. 75).

A. EXPERIMENTAL ANIMALS

1. Collection

In spring 1970 (March 3-8) I collected samples from Pinkut Creek, Fulton River, Morrison River, and Upper and Lower Babine rivers (Table 2) by shovelling into the gravel and netting alevins or eggs as they drifted downstream. They were taken in large plastic bags, one-third full of water and supplied with oxygen, to the Fisheries Research Board of Canada (FRBC) Rosewall Hatchery on Vancouver Island. This facility is 80 km NW of the FRBC Pacific Biological Station at Nanaimo, B.C. The trip took 36 hr.

In addition, eggs and milt from two females and three males were collected in Fulton River during the previous fall (early October, 1969). Half the eggs were fertilized with the combined milt at Rosewall Hatchery 40 hr after collection.

2. Culture

All fish were raised at Rosewall Hatchery. Tanks were supplied with well water, varying in temperature from 7.0 to 9.0 C in 1970, a range less than they would normally experience (from near 0 to about 18 C). The fish were in an enclosed building and could not see the sky.

Table 1. Distribution of experiments. The figures in brackets for outdoor tests are the actual number of test sessions. Three smolts were examined at each session for most of the season.

Lake population	River population	1970	1971	
		Indoor	Indoor	Outdoor
Nilkitkwa-North Arm				
	Upper Babine	18	33	78(33)
	Lower Babine	19	5	15(5)
Subtotal		37	38	93(38)
Morrison Lake				
	Morrison	13	35	73(33)
	Morrison[a]		6	17(6)
	Morrison[b]			61(29)
Subtotal		13	41	151(68)
Main Lake				
	Fulton	18	35	75(35)
	Fulton[a]		6	16(6)
	Fulton[a,c]		6	18(6)
	Pinkut		6	17(6)
Subtotal		18	53	126(53)
Total		68	132	370(159)

[a] Completely raised in small tanks.

[b] Holding group (retested every week).

[c] Collected as eggs in the fall.

Table 2. Summary of 1970 sampling operations.

Stock	Date	Location	Development	Approx. number
Pinkut Creek	March 3	200 m from mouth	Alevins-yolk sacs 1/2-3/4 absorbed	1,000
Morrison River	March 4	50 m below Morrison Lake	Alevins-yolk sacs 1/2 absorbed	1,000
Lower Babine River	March 5-6	1-2 km below Nilkitkwa Lake	Immature alevins	1,000
Upper Babine River	March 6	1.5 km below Babine Lake	60% immature alevins, 40% eggs	1,000
Fulton River	March 8	300 m from mouth	Alevins-yolk sacs 1/2 absorbed	1,200

Approximately natural photoperiods were maintained manually until November 16, 1970. Thereafter, a natural LD was automatically controlled by photocell. All sockeye were fed Oregon Moist Pellet commercial food.

From eggs and alevins collected in spring 1970, 400 survived from each of the Upper and Lower Babine, Pinkut, and Fulton samples and 250 from Morrison. Each group was randomly allocated two cylindrical tanks, 51 cm deep and 36 cm wide. Juveniles from one of the two tanks in each group were put into larger tanks (107 cm long, 48 cm wide, and 41 cm deep) on November 16, 1970. One large tank was randomly assigned to each group. These "large-tank" fish were housed in a light-proof room with photocell-controlled lights. Those remaining ("small-tank groups") were also given a photocell-controlled natural LD cycle.

In summary, 11 groups existed prior to the tests, classified by their origin and raising treatment: Upper Babine, Lower Babine, Morrison, Fulton, and Pinkut, raised from the fingerling stage in large tanks ("Main Stock groups"); the same origin groups but raised completely in small tanks; and Fulton egg stock (the group collected in autumn, p. 5) also raised entirely in small tanks.

3. Holding

Smolts were transported to the Biological Station on Friday of each week and tested the following Monday to Thursday. This gave them at least 2 days to recover before tests began. They were returned on the next trip to the hatchery on Friday. By returning subjects, some were probably tested more than once. This was acceptable since only a few individuals would be retested. $P = 0.16$ to 0.21 that an individual of one of the three most frequently sampled groups would be tested twice. Plastic bags containing the fish were kept in cooler containers with ice for the 1.5-hr trip.

Smolts were held in 120-ℓ glass aquaria at the Station, one aquarium for each group. Shields on the sides prevented undue disturbance. Automatic feeders were timed to give dry food at dawn and dusk; however, most fish did not feed. A photocell kept a natural LD.

B. EXPERIMENTAL PROCEDURE

I had to consider orientation cues in designing the experiments. Fish, including sockeye, are able to use the sun as an orientation cue for direction finding (Hasler et al. 1958; Braemer 1960; Schwassmann 1962; Winn, Salmon, and Roberts 1964; Groot 1965; Healey 1967; Goodyear and Ferguson 1969; Goodyear 1970). For this reason, I gave subjects a view of the sky in outdoor tests and provided a simulated sun for tests in the laboratory. The "sun" in the indoor tests was a stationary incandescent light. Several workers have used this method for other species (Kramer 1952; Schwassmann 1960, 1962; Landreth and Ferguson 1968). Since a responding animal constantly shifts its angle with the sun to compensate for the sun's movement, a stationary substitute will cause predictable deviations in its preferred direction. If this compensation occurs, indoor experiments will confirm that sockeye have a sun-compass mechanism.

I ran indoor and outdoor tests 3 times a day (12:00, 16:00, and dusk), at least 4 days a week, from April 13 to July 1. Dusk observations were 45 min before GMT of sunset. I tested one group a day and used fresh individuals for each test. The Main Stock groups tested every week were: (1) Fulton (on Monday); (2) Upper Babine (Tuesday); (3) Morrison (Wednesday); and (4) Holding (Thursday). These were Main Stocks, raised from fingerlings in large tanks. Groups 1 to 3 are referred to as "Major Groups" in the rest of the text. Holding smolts were Morrison fish from group 3, but held in the laboratory and retested every week. I tested several other groups on Saturday and Sunday after May 29. Each test lasted 15 min.

1. Testing apparatus

The outdoor apparatus (Fig. 2) consisted of three cylindrical acrylic drums resting on a stand with a movie camera monitoring behavior of the fish from underneath.[1] It was on the roof of a four-storey building at the Pacific Biological Station. The drums (30 cm in diameter and 30 cm high) had clear bottoms but painted sides to prevent visual interaction between smolts (Fig. 3). Eight vertical black stripes rising 15 cm from the bottom and symmetrically placed inside the drums gave a more patterned environment. Temperatures were partially controlled by putting the drums in a large acrylic tank filled with water and this tank fitted over a hole in a platform. The platform also supported metal shields around the tanks and a black plastic curtain, closed at the bottom, hung down from the hole. The platform with its tanks, shields, and curtain, could be rotated on the stand. The lens of the movie camera (Braun-Nizo S-56 Super 8) projected through a central hole in the curtain's bottom shield and took time-lapse pictures: one frame/sec (Fig. 4). The camera top, hence the top of the film frames, pointed to True North.

The following changes in apparatus were made for laboratory tests:

(1) Only one drum tank was used (30 cm diameter).

(2) The drum sides were transparent and only 20 cm high (Fig. 5).

(3) The metal shields were removed and room features occluded by a translucent acrylic hood over the drum tank (Fig. 6). The hood was 1/8 in Plexiglass, W2067, with 72% light transmittance.

(4) A 1000 W medium-wide flood lamp (Sylvania 1000/R60/MWFL) simulated the sun. It was clamped on an arc-shaped rack, 147 cm from the drum and at the solar altitude for the time of day (Fig. 6). Figure 7 shows the light intensity patterns in the center of the drum for mid-May. The light gradually lost power, so intensities averaged 6% greater at the start of tests in April and 6% less at the end of the season in June.

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[1] Only one tank was used before May 10.

[illegible] 19:00, and dusk), at least [illegible] observations were [illegible] and used fresh individuals [illegible] every week were: (1) [illegible] (Wednesday); and (2) [illegible] raised from fingerlings in large [illegible] groups" in the rest of the [illegible] but held in the laboratory and [illegible] other groups on Saturday and Sunday [illegible]

[illegible]

[illegible] three cylindrical acrylic [illegible] behavior of the [illegible] building at the [illegible] and 77 cm high) had [illegible] from the bottom and [illegible] environment. Temperature [illegible] in a large acrylic tank [illegible] The plastic [illegible] a black plastic curtain [illegible] platform with its tanks [illegible] The lens of the [illegible] central hole in the [illegible] (Fig. 4). The [illegible] depth.

[illegible] laboratory tests)

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Fig. 2. Outdoor test apparatus on the roof of the F.R.B.C. Pacific Biological Station. The canvas cover which enclosed the base of the tank has been removed to show the plastic curtain shield and camera mounting. Approximate scale: 1:30.

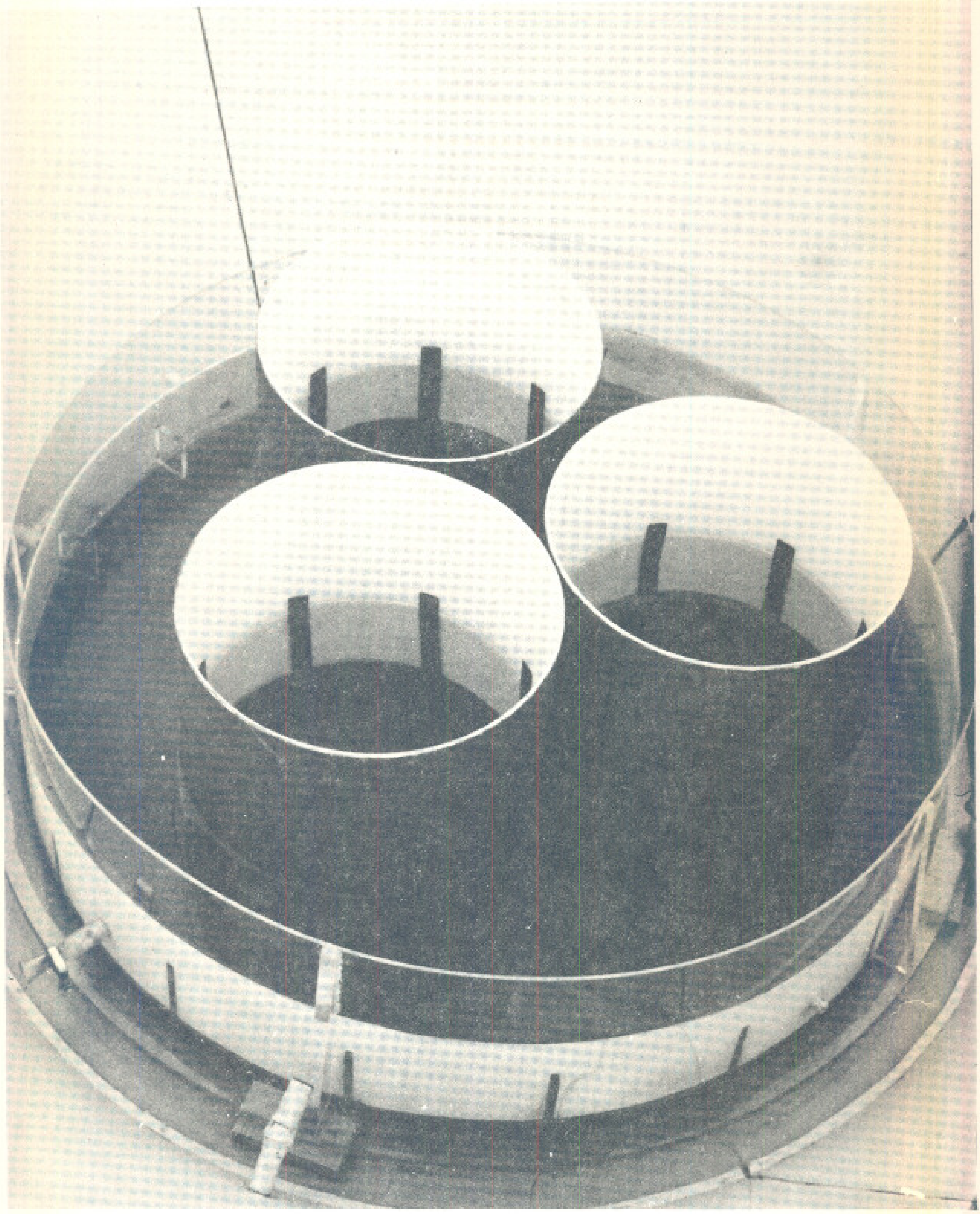


Fig. 3. Test tanks in outdoor tests. Approximate scale: 1:10.

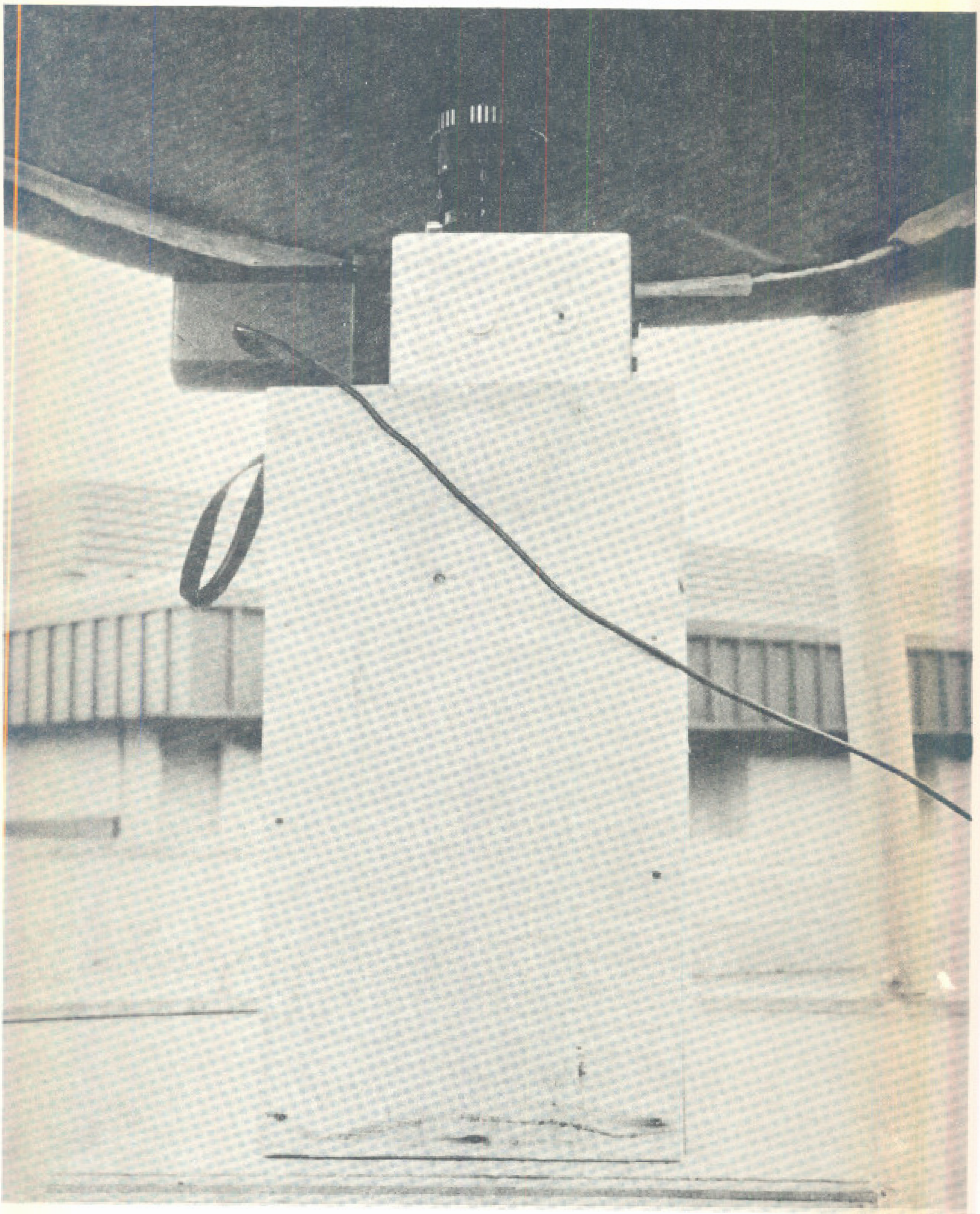
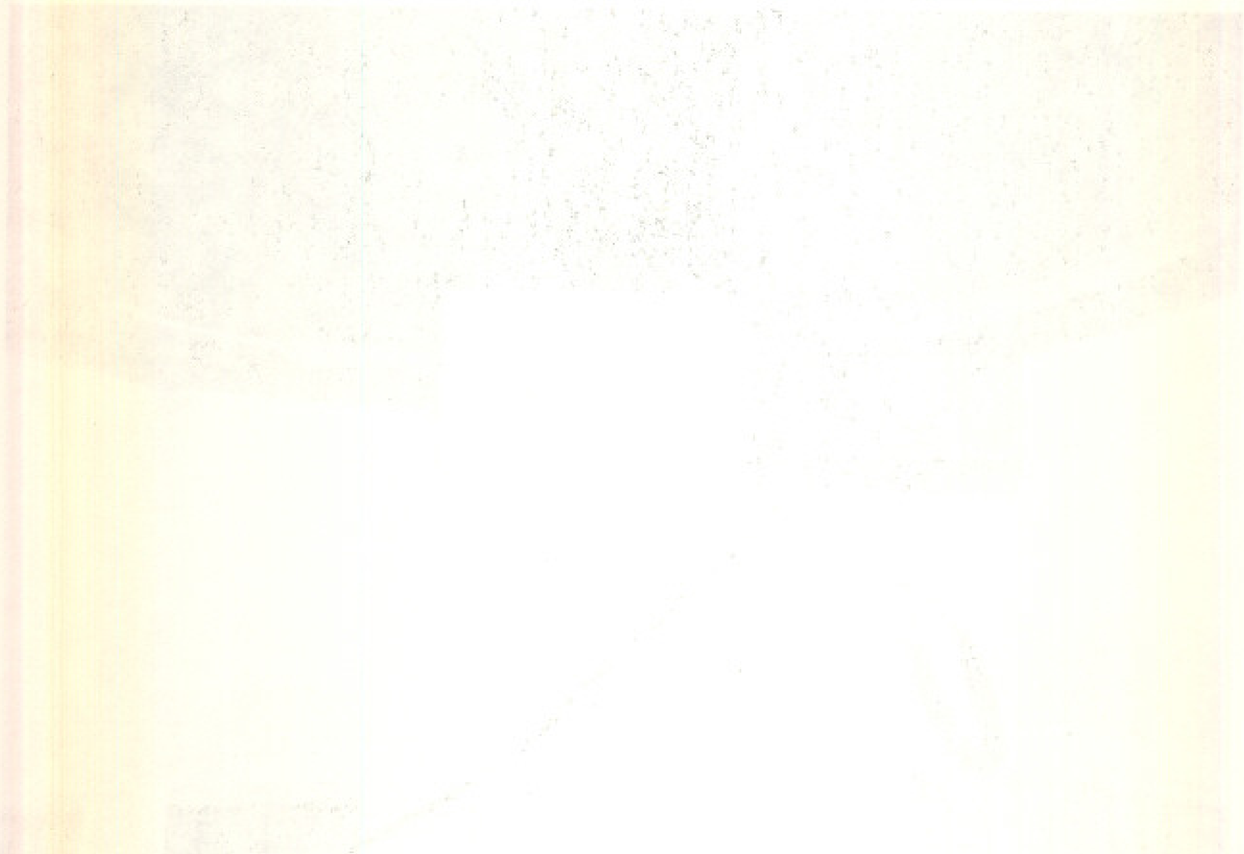


Fig. 4. Mounting of movie camera. The plastic shield has been raised so the lens can be seen. The top of the camera points towards True North. The cord is the power supply and goes to an electric timer. Approximate scale: 1:4.6.



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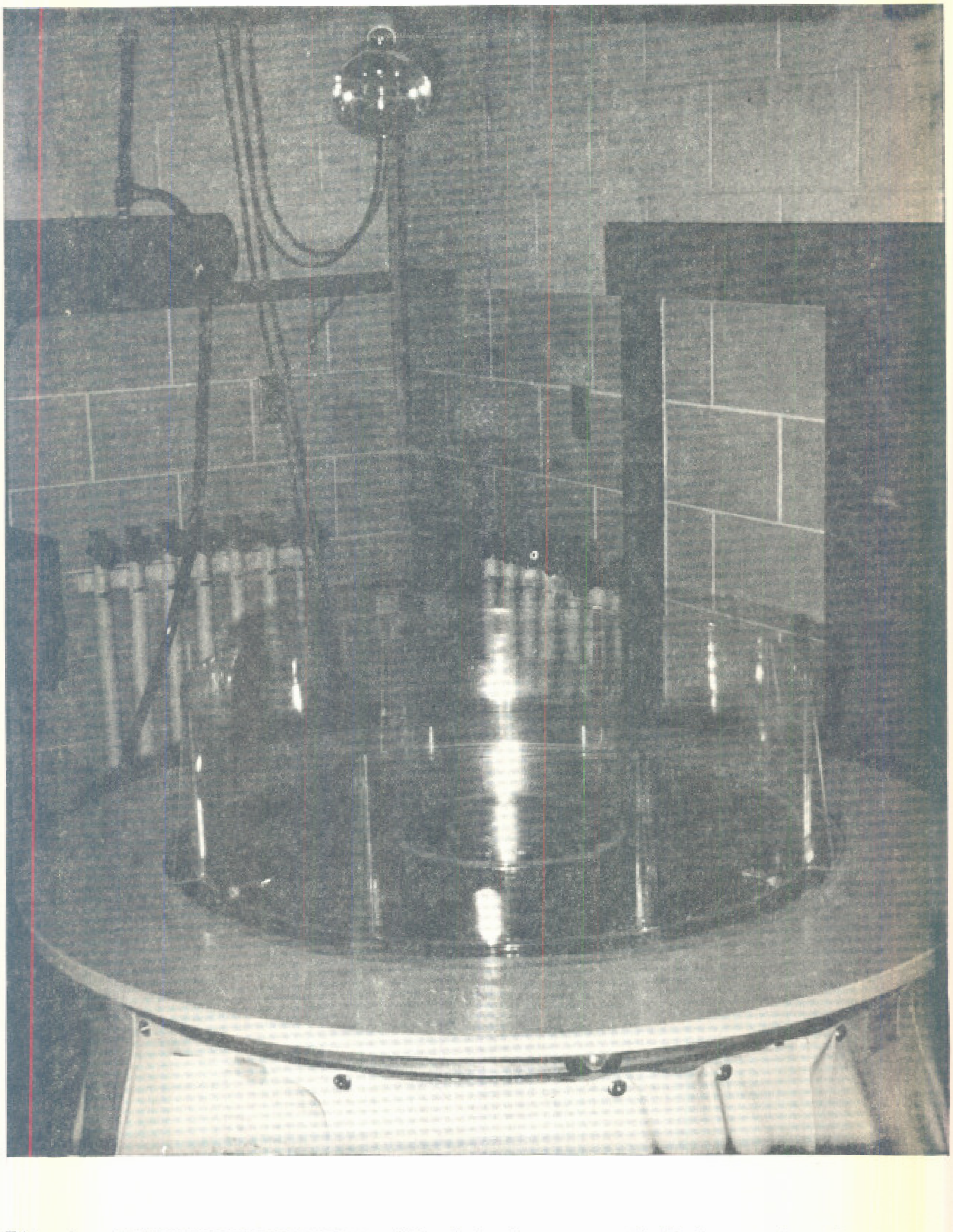

Fig. 5. Indoor test apparatus without tank cover. A fish was placed in the clear acrylic drum tank in the center. The lamp in the background is the artificial sun. Approximate scale: 1:10.

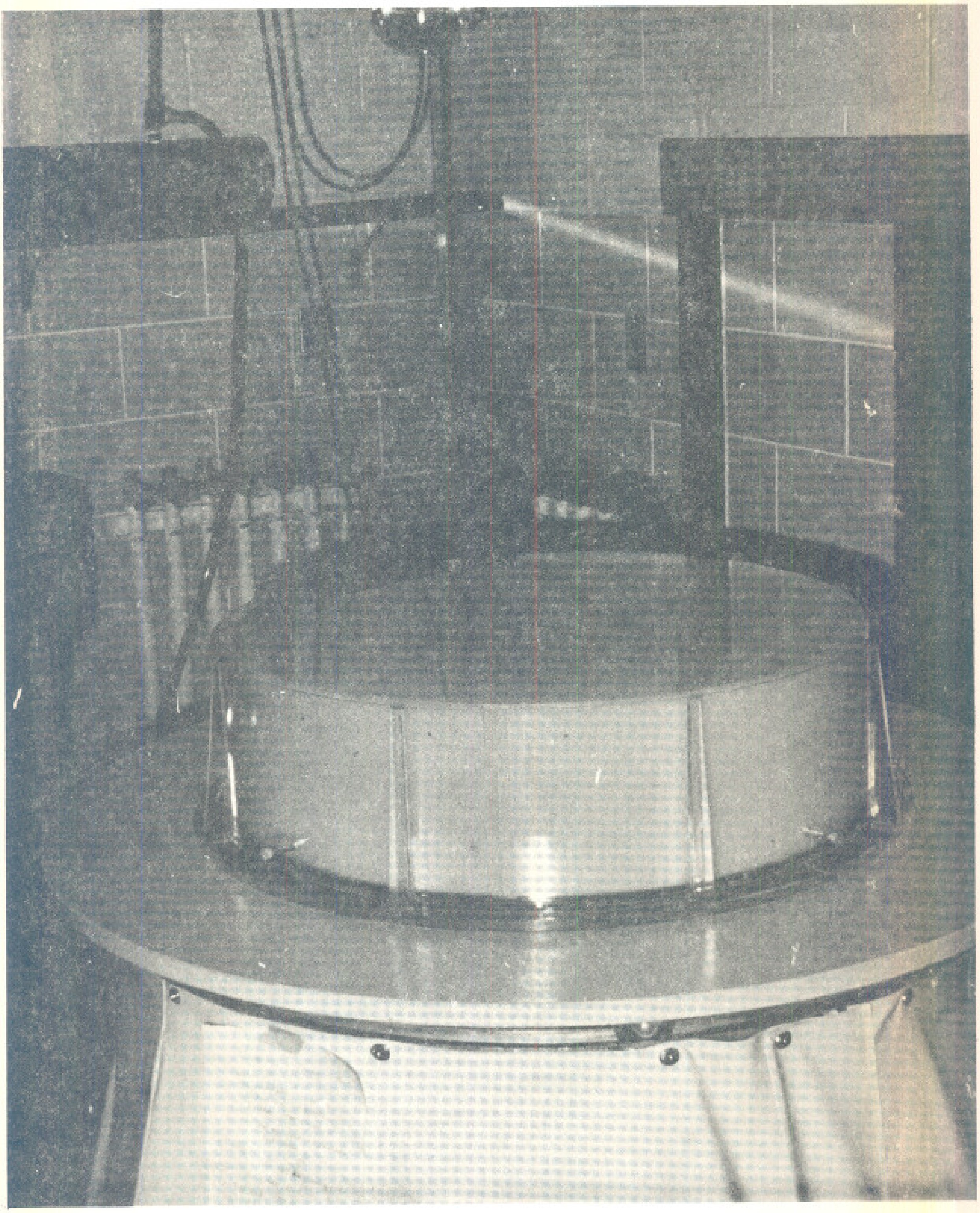

Fig. 6. Indoor apparatus with transluscent cover in place. Approximate scale: 1:10.

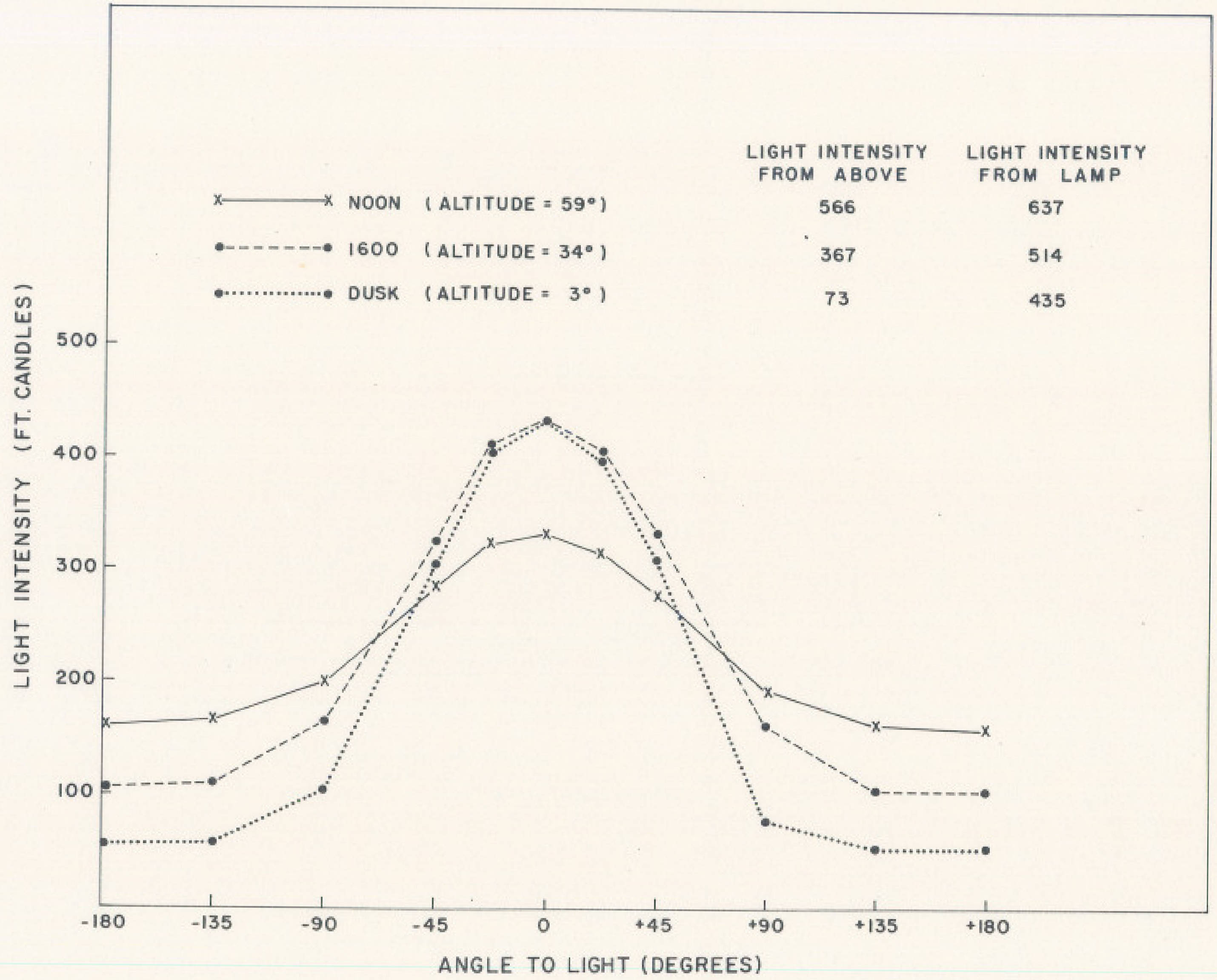

Fig. 7. Distribution of light intensities in the indoor test tank at different test times. Abscissa: angle between a horizontally directed light meter (placed at tank center) and the artificial sun. Light intensity from above: meter directed vertically from center of the tank. Light intensity from lamp: meter directed towards the lamp from center of the tank.

2. Testing procedure

Outdoor tests

Marks on the test apparatus may affect directional preferences (Hasler 1956) so the apparatus was rotated randomly before introducing the fish. Before May 10, when only one drum (and one smolt) was used, I turned the whole platform with its metal shields and plastic curtain. When testing three smolts, I rotated the drum tanks before every test and only turned the platform twice. Rotations did not seem to influence preferred directions.

A smolt was put in each drum tank 2 hr before the observations began. The drums were filled 15 cm deep which gave the smolt a 90° view of the sky from the center of the water surface. Temperature differences between holding aquaria and drums were minimized by first cooling water for the drums in a 205-ℓ reservoir beside the stand (Fig. 2, p. 11). There was no water circulation so temperatures usually rose during a test (mean change = 2.8° ± 2.0). The increase varied with test time: 4.4° (± 2.1) at 12:00, 3.4° (± 1.7) at 16:00, and 1.5° (± 1.0) at dusk. After the adaptation period, I started the camera from outside the stand and let it run 15 min.

Weather observations were made at the beginning of the adaptation period and during the test (Table 3). The radiation sensor was about 20 m from the stand and the thermograph was at an Atmospheric Environment Service weather station, 100 m away. "Past weather" means the weather conditions (e.g. rain) in the last 6 hr or since the last observation, whichever was less.

Indoor tests

Preparation for indoor tests involved filling and rotating the tanks and adjusting the light altitude. Water in the cooling tank and drum (15 cm deep) was pumped from an aquarium which had the same water supply as the holding aquaria. The mean temperature difference was 0.8 C (± 0.4). I rotated the platform before putting fish in the drum. Rotations did not seem to affect preferred directions in these tests either. The light's altitude was adjusted using altitude tables (U.S. Navy Hydrographic Office 1952) and ranged during the season from 49 to 63° at noon and 26 to 37° at 16:00. Altitudes were less than 5° at dusk.

A fresh smolt was put in the drum and covered with the translucent hood. No one entered the room until after the test and the simulated sun was the only light source during this time. Water temperatures rose 5.2 C (± 0.5) at noon, 3.0 C (± 0.6) at 16:00, and 4.2 C (± 0.5) at dusk. After 2 hr I started the camera from next door.

C. DIRECTIONAL MEASUREMENTS

Films were analyzed with a time-motion projector (Kodak Ektagraphic MFS-8) and Trilateral Reader (Fig. 8 and 9). The Reader was used to measure head and tail positions of the fish. The dorsal fin was used instead of the tail when the body axis was bent, assuming that the orientation of the anterior body was most important. Positions were recorded on paper tape as string-lengths

Table 3. Observation and recording of weather.

Variable	Instrument	Recording method
1. Air temperature	Atmospheric Environment Service thermograph	Degrees Fahrenheit
2. Wind direction[a]	Compass	To nearest 10°N
3. Wind speed	Anemometer (Sims "BBK")	Beaufort scale
4. Cloud type[a]	-	0-9 number code
5. Cloud height	-	1-6 scale
6. Cloud cover[a]	-	0-8 oktas
7. Sun visibility	-	0-4 scale
8. Moon visibility	-	Brightness (0-3)x phase (0-3)
9. Star visibility	-	0-4 scale
10. Present weather[a]	-	0-99 number code
11. Past weather	-	0-9 number code
12. Light intensity	Light meter (Gossen "Traasix")	Foot-candles
13. Atmospheric radiation	Atmospheric Environment Service Eppley Pyranometer	Langleys/hour

[a] Coded as in the Canadian Oceanographic Data Center's "Data Summary Coding Form" (MTS-149-Feb.-65).

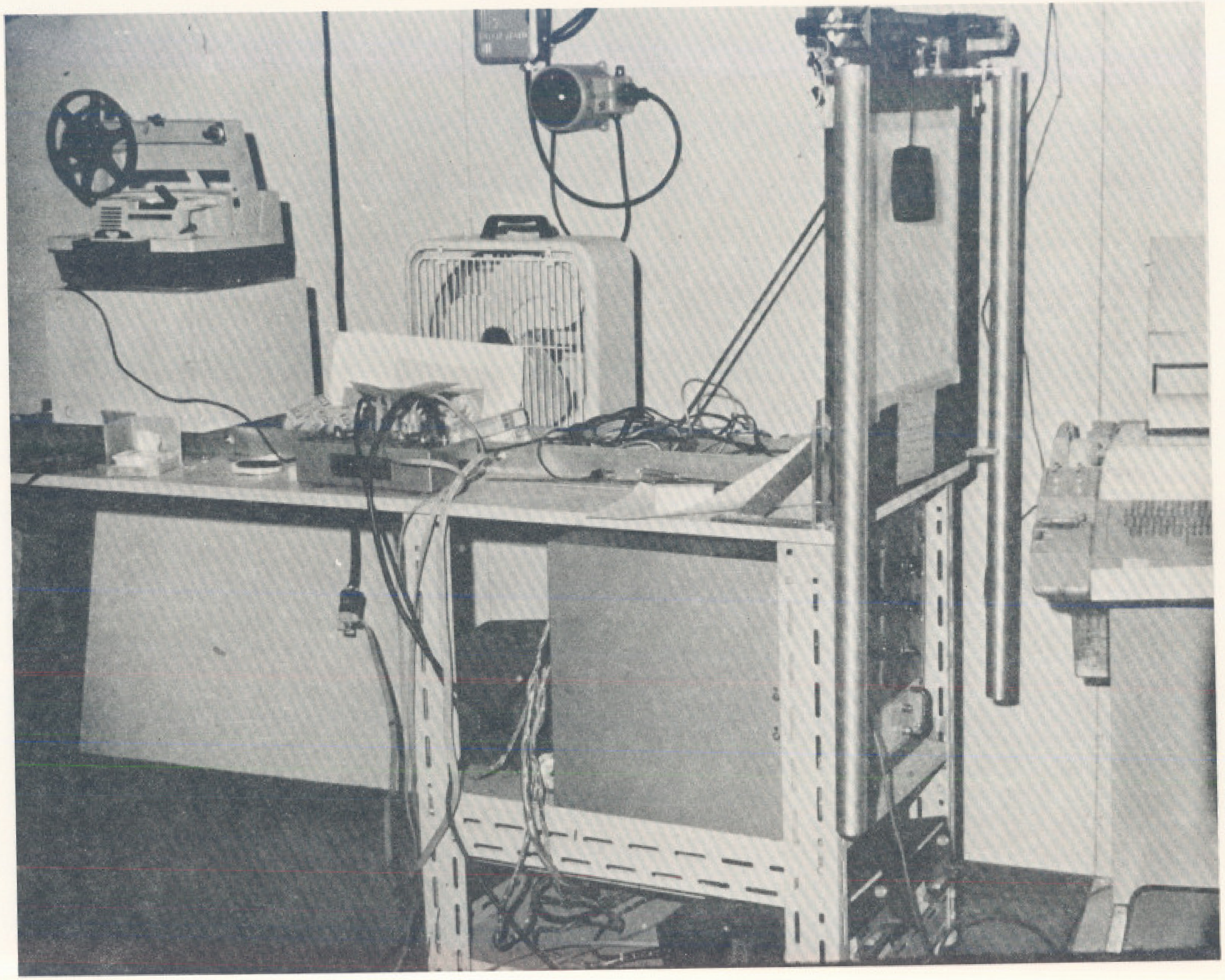

Fig. 8. Apparatus for measuring directions. The projector is on the left, the Trilateral Reader screen on the right. Positions are measured with the electronic devices below the screen and are transmitted to the teletype unit (far right) for output. Approximate scale: 1:17.

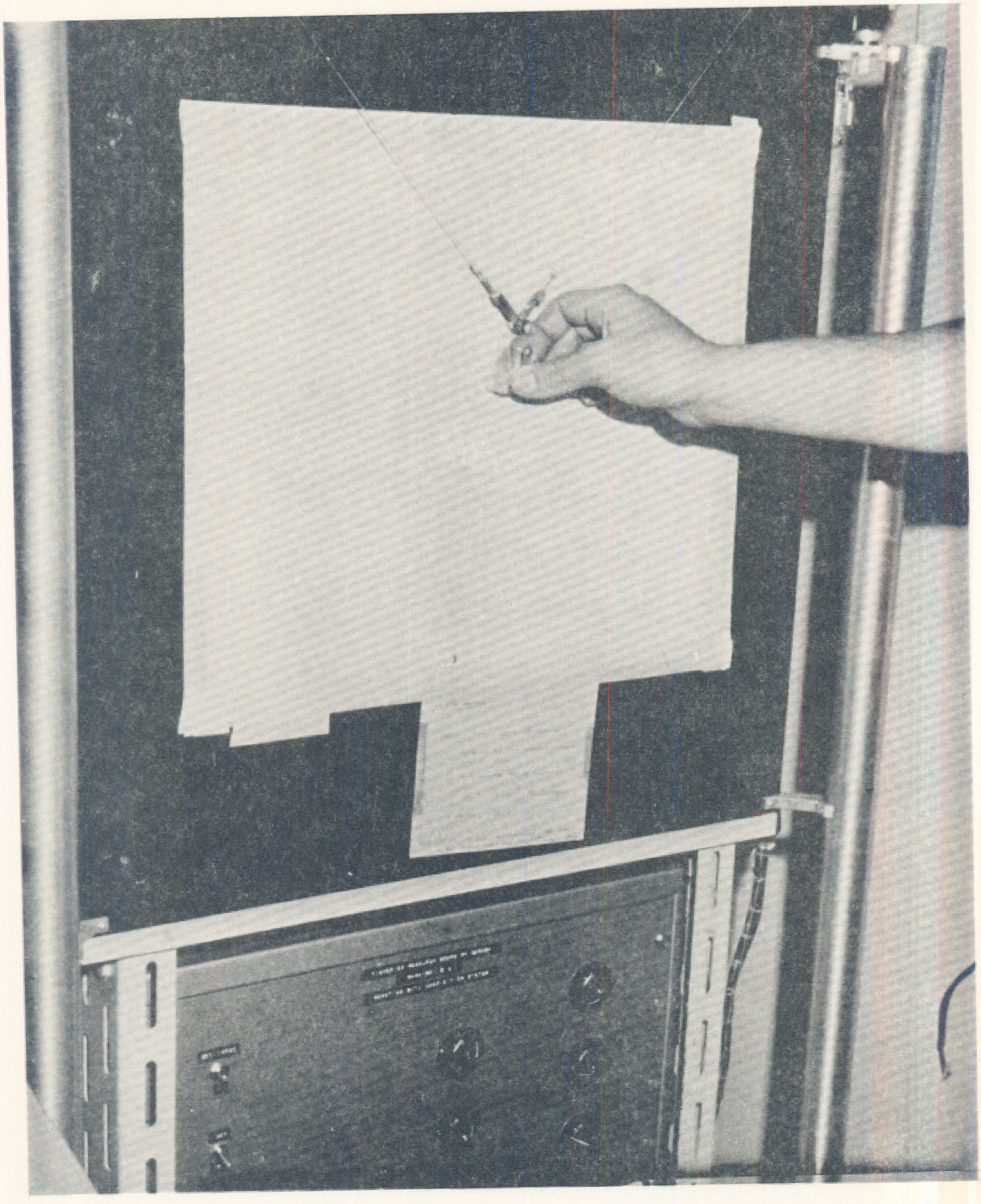

Fig. 9. Close-up of the Trilateral Reader screen. The position of the pointer in the person's hand is quantified by measuring the lengths of the two strings.

between the pointer and two potentiometers (Simpson and Groot 1972). Accuracy was ±1 mm over 600 mm (the diagonal of the screen).

The operator recorded head and tail positions of the smolt after it had been stationary for 3 sec (3 frames). Groot (1965) used the same "pointing" criterion to determine directional tendencies. Measurements were taken at 3-frame intervals until the subject moved again. This involved some subjectiveness since a smolt often slowly changed direction or slowly moved forwards or backwards. Its direction was recorded if the head moved less than 1 to 2 cm in the 3-sec period.

This subjective evaluation had little effect on results, however. Two tests analyzed first in April and again in June showed a reduction in pointings of 44% and 72.5% because the observer was much more selective. However, the strengths of orientation, strong in one fish and weak in the other, as well as the mean directions were virtually unchanged. Personal expectations about the smolts' orientation (see Harden-Jones 1968) probably did not bias the results toward the hypothesized directions because (1) the operator did not know what the direction should be for a particular group at the test date, and (2) geographic directions are difficult to determine on the film.

D. STATISTICAL ANALYSIS

I wrote several computer programs to do the following operations (Simpson and Groot 1972):

(a) Preparation of data

1. Data retrieval from paper tape.
2. Calculation of Cartesian coordinates.
3. Calculation of compass directions of pointings.
4. Determination of independent directions.

(b) Statistical analysis

1. Calculation of statistics describing the circular distribution of independent directions.
2. Comparison with various theoretical distributions and directions using significance tests.

Programs also summarized groups of tests, using the resultant vector of each test as data.

1. Determination of independent data

When measurements of a dynamic object are taken close together temporally, successive values may depend on previous values. Misleading interpretations obviously follow: in orientation, the subject's inertia biases the results towards stronger orientation. Workers usually take the mean direction of an experiment as one data point (sample size = number of experiments). There are two disadvantages to this: (1) it requires many experiments to obtain adequate sample sizes, and (2) it only considers one statistic, the mean direction. The first limitation is particularly serious because most orientation studies must be completed within a relatively short migration period. The second disadvantage means that the strength of the individual's orientation is not considered, and strongly oriented animals are not given greater weight. Some workers partly rectify this by eliminating experiments with orientation weaker than some arbitrary level, leading to further losses of information.

I used a technique developed by Hamilton (Hamilton 1966; Marler and Hamilton 1966) to find what the minimum temporal spacing had to be before directional preferences became independent. The longer the time interval between dependent directional choices, the more different these choices are. An interval is finally reached, however, after which differences no longer increase appreciably because the directions are independent of each other. The first step is to calculate the average difference between successive directions, then between directions two spaces apart, etc. This is given by the equation

$$\overline{X}_t = \frac{\sum_{I=1}^{N-t} \left| X_I - X_{I+t} \right|}{N - t}$$

where the data points are $X_1, X_2, \ldots X_N$ and the equation is solved for $t = 1, 2, 3 \ldots$ spaces. Temporal spaces between the data points varied in length because pointings were not recorded when the fish was active. The procedure is still applicable, however. The second step is to determine when the average differences are not increasing substantially. I used Hamilton's criterion that independence is assumed when $\overline{X}_t$ does not change by more than 10% in two successive increments of the interval.

Plotting the average difference for each interval gives a useful description of the individual's orientation. Measurements become independent near the point of inflection. If the inflection occurs at about 90° average difference, and especially if t is still small, the animal probably oriented randomly. This is because random dispersion of directions over the complete range (180°) will have a mean near 90°. If average differences increase slowly the smolt will have tightly grouped pointings. Randomness of preferences is found more easily using methods described below but these graphs can give a more detailed picture of orientation with respect to time.

Once the independence interval (equal to the number of intervening measurements plus one) is found the data are divided into groups of this interval size. The program calculated the mean direction by vector addition (see below) for each interval group and these became the independent data.

2. Descriptive statistics

Conventional statistics were designed to describe linear distributions and are generally unsatisfactory when the data are circular. Special methods have been developed to treat circular data as radius vectors (Batschelet 1965). The direction (α) and strength ($\bar{a}$) of the mean vector describe the distribution's central tendency and dispersion. The mean vector is calculated by vector addition of the data (ξ_i, i = 1, 2, . . . n, where n is the number of independent directions):

$$W = \sum_{i=1}^{n} \sin \xi_i \qquad V = \sum_{i=1}^{n} \cos \xi_i$$

$$\alpha = \arctan (W/V).$$

α is the direction of the resultant vector and its magnitude is:

$$R = \sqrt{W^2 + V^2}.$$

The mean vector has the same direction but its magnitude is:

$$\bar{a} = R/n .$$

$\bar{a}$ ranges from 0 to 1: 0 for a perfectly uniform distribution and 1 indicating an unvarying directional preference.

Smolts may prefer directions 180° opposite and the resulting distribution creates problems in vector analysis since the modes tend to cancel each other in vector addition. All data were checked for bimodality by Krumbein's (1939) transformation, i.e. multiplying each direction by two and subtracting 360° from the product if it exceeds 360°. This reduces the dispersion in bimodal distributions by creating a single mode. If $\bar{a}$ is greater after the transformation a bimodal distribution is assumed (Groot 1965). If α_2 is the mean direction for the transformed distribution, directions of the modes are $\alpha_2/2$ and $\alpha_2/2 + 180°$.

Groups of tests were summarized by combining all independent directions and the circular statistics, transformations, and significance tests were recalculated. Groups of tests were also summarized by the traditional method using only mean directions for each test.

3. Significance tests[2]

The first question mentioned in the Introduction (p. 1) can be rephrased as "Are the directions uniformly distributed?". I used the modified Rayleigh test (Greenwood and Durand 1955) to test the null hypothesis that they have a uniform distribution. The statistic, $Z = R^2/n$, was compared to critical values found in Batschelet (1965).

In the second question, I wanted to see if the central tendencies of the distributions were significantly different. My data seriously violated the conditions of Watson and William (1956) parametric F-test and the large sample sizes precluded using non-parametric tests (Batschelet 1965). A multi-sample randomization test was designed instead, which used the statistic:

$$B = \Sigma R_i - R$$

where R_i are the resultant vector lengths of the samples and R is the resultant vector length for the combined samples. This is a simplification of the statistic used by Watson and Williams (1956). B will be 0 ($\Sigma R_i = R$) when all resultants are in the same direction. It increases with greater dispersion between groups (because R decreases) and with less dispersion within groups (ΣR_i increases). Sample sizes are considered also since the resultant vector length for a sample will tend to increase with increasing n.

The samples are pooled after B is found. Directions are drawn at random and without replacement from this pool to form new groups of the same size and number as the originals. This is repeated for a few hundred trials, recalculating B each time. If the actual B value exceeds 95% of the B's for randomly selected samples, the groups are significantly different ($P < .05$).

The third question asks if the mean directions differ significantly from theoretical directions. A test suggested by Stephens (1962) was used which is based on X, the component of the resultant vector in the theoretical direction:

$$X = R \cos (\alpha - \theta_o)$$

where α is the mean direction and θ_o is the theoretical direction. A critical value R_o was found from the equation:

$$R_o = \sqrt{X^2 + \chi_1^2 \frac{n}{2}}$$

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[2] In this report, a significance level between 1 and 5% is denoted by "*," less than 1% by "**," and less than 0.1% by "***."

(Stephens 1962). χ_1^2 is the upper critical value of the chi-square distribution with one degree of freedom and significance level of 1% or 5%. If the length of the resultant vector (R) is greater than R_o, the mean direction is significantly different from the theoretical direction (Batschelet 1965).

RESULTS

Appendix C (p. 103) summarizes the results for each test. Mean directions, orientation strengths, and activity were examined in relation to these variables:

(1) Stream origin of samples.

(2) Test time (date and time of day).

(3) Test treatment, especially indoor vs. outdoor tests.

I will only discuss results for Main Stock groups.

A. QUESTION 1: DO SUBJECTS ORIENT?

Since this is the first attempt to study non-conditioned migratory orientation of artificially reared smolts, the answer to this crucial question was particularly uncertain. The first requirement is that individual fish orient non-randomly. Secondly, fish from the same stream must prefer similar directions.

1. Individual orientation

Strength of orientation by individuals was examined by using $\bar{a}$, a statistic indicating dispersion around the mean (p. 31). Activity and association between successive pointings are also related to this question and are discussed in Appendix B (p. 93).

Table 4 shows how many smolts were significantly oriented ($P < .05$, Rayleigh test) in each origin/time/location category. There were 300 significant orientations out of 431 Main Stock tests (70%), indicating that smolts usually had definite directional preferences.

Time of day

The column totals in Table 4 show that the proportion of indoor tests with significantly strong preferences was 76%, 84%, and 84% for 12:00, 16:00, and dusk, respectively. Test time had little effect indoors apparently. In outdoor tests, however, the corresponding proportions (73%, 68%, and 56%) were significantly different from each other ($\chi^2 = 6.97$*).

Table 4. Frequency of 1971 Main Stock tests with significantly strong orientation ($P < .05$). Numbers in brackets are the percent of total number of tests in the category (shown in Table 5).

	Indoor				Outdoor				
Origin	12:00	16:00	Dusk	Total	12:00	16:00	Dusk	Total	Total
Fulton	10(91)	9(75)	10(83)	29(83)	19(73)	17(65)	12(50)	48(63)	77(69)
Upper Babine	7(64)	9(90)	10(83)	26(79)	18(69)	14(52)	15(63)	47(61)	73(66)
Morrison	10(83)	10(91)	9(90)	29(88)	17(77)	17(68)	14(54)	48(66)	77(73)
Lower Babine	0(0)	2(100)	2(100)	4(67)	5(83)	6(100)	2(67)	13(87)	17(81)
Pinkut	2(100)	1(50)	1(50)	4(67)	6(100)	2(33)	3(60)	11(65)	15(65)
Morrison (Holding)					8(57)	21(88)	12(55)	41(68)	41(68)
Total	29(76)	31(84)	32(84)	92(81)	73(73)	77(68)	58(56)	208(65)	300(70)

The column totals of Table 5 show that mean $\bar{a}$ values follow this pattern as well. A proper analysis requires examination of possible interactions between all three factors (time, location, and origin). For example, the previous results suggest that time effects are different in indoor and outdoor test series. I explored this by doing an unbalanced analysis of variance (Bram 1970) using these three factors. Only the Major Groups were used since there were relatively few Lower Babine and Pinkut tests. $\bar{a}$ values had a platykurtic distribution so I transformed them to arcsine $\sqrt{\bar{a}}$. The new distributions closely approximated normal distributions and variances were homogenous (Barlett's test $P \gg .05$).

ANOVA results are given in Table 6. The null hypothesis that time affects strength of orientation the same in both test series, or the effect of location is the same at all times, cannot be rejected at the 5% level ($F = 2.51$, $.10 > P > .05$). Even though it is insignificant at the 5% level the size of this F value means that the main effect for time should be interpreted cautiously. Indoors, mean $\bar{a}$ values for 12:00, 16:00, and dusk were .64, .65, and .70, respectively, but they declined in outdoor tests: .60, .58, and .55. As a precaution, I analysed each test series separately, using one-way ANOVA, and found that these means were not significantly different between test times indoors ($F = 0.65$) or outdoors ($F = 2.02$).

The effect of time was complicated, therefore. The proportion of smolts with significantly strong preferences declined through the day when they were tested outdoors but not when tested indoors. Mean orientation strengths followed the same pattern but the differences were not significant in either series. Neither could I accept the hypothesis that time affected indoor and outdoor smolts differently in this respect.

Location

Tables 4 (p. 34) and 5 show that 81% of all indoor smolts were oriented and the mean $\bar{a}$ statistic was 0.66. The corresponding figures for outdoor tests are 65% and 0.58. This marked reduction in orientation strength when smolts were tested outdoors was highly significant ($P < .001$), as seen in Table 6 (p. 37). It follows from the discussion on time effects that the difference between test series was greatest at dusk. The biological significance of time and location effects will become apparent when orientation cues are discussed.

Stream origin

One could reasonably expect Babine Lake populations to differ in their members' orientation strengths. For example, Upper and Lower Babine populations probably do not require as strong an orientation to find the outlet as Morrison River progeny. Tables 4 (p. 34) and 5 reveal little difference between samples, however. Origin was quite insignificant in the analysis of variance for Major Stocks (Table 6).

Table 5. Mean $\bar{a}$ values for 1971 Main Stocks. Figures in brackets are number of tests ($\bar{a}$ values) in each category.

	Indoor				Outdoor				
Origin	12:00	16:00	Dusk	Total	12:00	16:00	Dusk	Total	Total
Fulton	.67(11)	.56(12)	.75(12)	.66(35)	.62(26)	.61(26)	.47(24)	.57(76)	.60(111)
Upper Babine	.59(11)	.73(10)	.69(12)	.67(33)	.55(26)	.49(27)	.58(24)	.54(77)	.58(110)
Morrison	.66(12)	.67(11)	.71(10)	.68(33)	.65(22)	.58(25)	.51(26)	.58(73)	.61(106)
Lower Babine	.25(2)	.81(2)	.55(2)	.54(6)	.56(6)	.82(6)	.55(3)	.66(15)	.63(21)
Pinkut	.96(2)	.55(2)	.59(2)	.70(6)	.69(6)	.38(6)	.63(5)	.56(17)	.60(23)
Morrison (Holding)					.55(14)	.65(24)	.63(22)	.62(60)	.62(60)
Total	.64(38)	.65(37)	.70(38)	.66(113)	.60(100)	.58(114)	.55(104)	.58(318)	.60(431)

Table 6. Three-way analysis of variance to test differences in orientation strength between time and location categories of the three Major Groups. Arcsine $\sqrt{a}$ was the measure of orientation strength.

Source of variation	df	SS	MS	F
Between locations	1	3,476.0	3,476.0	13.30***
Between origin groups	2	252.5	126.3	0.48
Between times	2	282.8	141.4	0.54
Location × origin	2	43.7	21.9	0.08
Location × time	2	1,312.2	656.1	2.51
Time × origin	4	849.1	212.3	0.81
Location × time × origin	4	2,069.0	517.5	1.98
Error	309	80,771.0	261.4	
Total	326	89,171.2		

Holding treatment

Several Morrison fish were retested outdoors throughout the season to see if they oriented differently with experience. Row totals for outdoor tests in Table 4 (p. 34) show that the proportion of smolts with significantly strong orientations was virtually identical for the major Morrison stock (66%) and the Holding group (68%). Neither was the mean $\overline{a}$ for Holding (0.62) significantly different from the 0.58 value for the parent group ($F = 1.08$, arcsine transformation of $\overline{a}$). I conclude that experience of previous tests and view of the sky did not strengthen individual orientation.

Time of season

I calculated linear regressions of arcsine $\sqrt{\overline{a}}$ versus date to assess seasonal effects on individual orientation strengths (Table 7). Seven of the nine indoor cells had positive regression coefficients, four of which represented significant increases in orientation strength. In outdoor groups, five had positive coefficients and seven were negative. None were significant. Note, in particular, that Holding smolts did not strengthen orientation with retesting.

It is not clear why smolts tested later in the season had stronger preferences in indoor tests. The same stocks did not change throughout the season when tested outdoors.

2. Orientation of samples

What was the total variation, including variation between individuals in each sample? To answer this question, I calculated mean vectors by vector addition of all independent directions in each group (Table 8 and Fig. 10).

Time of day

I analysed time effects by calculating mean vectors of origin/test treatment/time groups for the three Major Stocks. Median Z values for indoor and outdoor groups at 12:00, 16:00, and dusk were 1.98, 7.22, and 3.52.[3] Directional consistency between smolts was greatest at 16:00, therefore. Both indoor and outdoor groups of Upper Babine and Morrison subjects had a peak at 16:00. Fulton fish were more consistent at dusk in both test treatments. Unfortunately, I could not test the significance of these differences between times because the data had several bimodal distributions and Z itself is not normally distributed.

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[3] $\overline{a}$ values should not be compared when samples differ in size because their significance rapidly changes with n.

Table 7. Regression coefficients of 1971 test $\bar{a}$ values regressed on date. $\bar{a}$ values were transformed to arcsine $\sqrt{\bar{a}}$ to approximately normalize their distribution.

	Indoor			Outdoor		
Origin	12:00	16:00	Dusk	12:00	16:00	Dusk
Fulton	+.468*	+.062	+.468*	-.138	-.193	+.011
Upper Babine	-.139	+.590*	+.399*	-.005	+.079	+.235
Morrison	+.202	-.213	+.057	-.182	-.128	+.231
Morrison (Holding)				-.107	+.228	-.206

Table 8. Summary of orientation by 1971 Main Stock samples. Bimodal axes are indicated where $\bar{a}$ for the distribution of doubled angles exceeds the original $\bar{a}$ (p. 31).

Origin	Indoor tests				Outdoor tests				Combined tests			
	N	Mean	$\bar{a}$	Z	N	Mean	$\bar{a}$	Z	N	Mean	$\bar{a}$	Z
Fulton	572	301	.11	7.19**	1605	283	.02	0.42	2177	296	.04	3.67*
						127-307	.03	1.14				
Upper Babine	641	258	.06	2.60	1398	222	.01	0.05	2039	252	.02	1.11
						82-262	.07	6.38**		77-257	.06	7.59**
Morrison	675	198	.09	5.13**	1614	224	.08	11.08**	2289	216	.08	15.47**
		143-323	.13	10.98**								
Lower Babine	109	165	.16	2.76	418	302	.20	17.54**	527	293	.14	10.40**
Pinkut	81	136	.53	22.86**	367	122	.18	11.62**	448	128	.24	25.83**
Morrison (Holding)					1240	55	.10	13.48**				
						64-244	.16	32.82**				

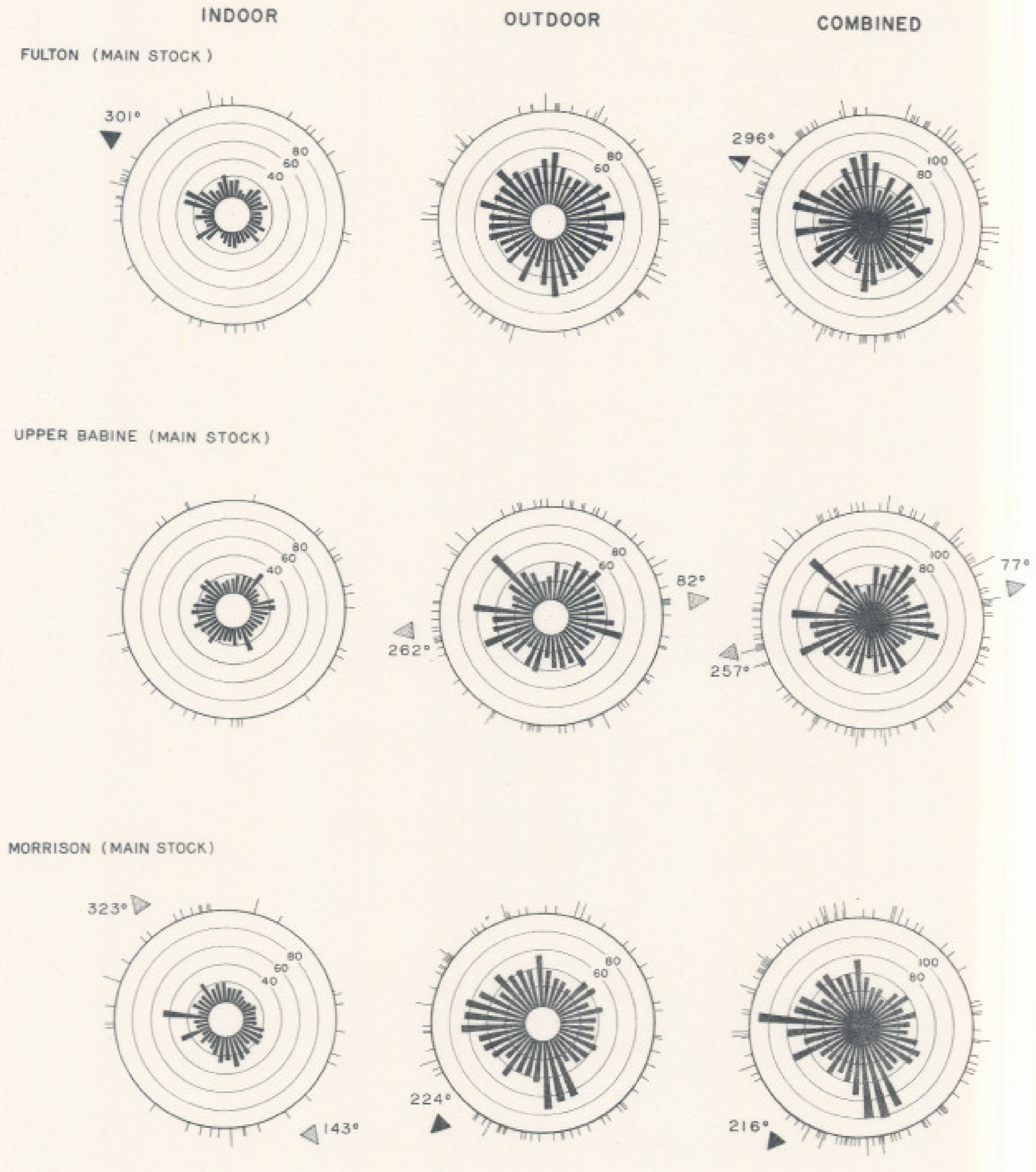


Fig. 10. Distribution of independent directions (central histogram) and test mean directions (on perimeter) for 1971 Major Groups. Longer lines on the perimeter indicate superimposed mean directions. Black triangle: mean direction of unimodal distribution of independent directions differing from uniformity at the 1% level, half-black triangle: 5% > P > 1%, and no triangle: uniform distribution (P > 5%). Dotted symbols are used for bimodal distributions.

Location

Most samples had significantly strong unimodal preferences when tested indoors (Table 8, p. 40). Only Upper and Lower Babine samples had uniformly distributed preferences. It may be significant that both are from the outlet area population. The distribution of independent directions in Fig. 10 (p. 41, central histograms) and especially the distribution of test mean directions (on perimeters) show that even significant sample preferences were not very strong in the Major Groups.

It is important to note that directions for indoor tests were measured relative to the lamp. The lamp bearing used in calculations is assigned the direction of the sun at test time. That some preferences occur may mean that subjects are compensating using a sun-compass mechanism.

Analysis of Rayleigh statistics (Z) in Table 8 suggests that outdoor preferences were not as strong as indoors. The outdoor smolts mainly differed by having more bimodal tendencies. In the case of Morrison, the modes were 110° apart in outdoor tests, very similar to the indoor distribution (Fig. 10).

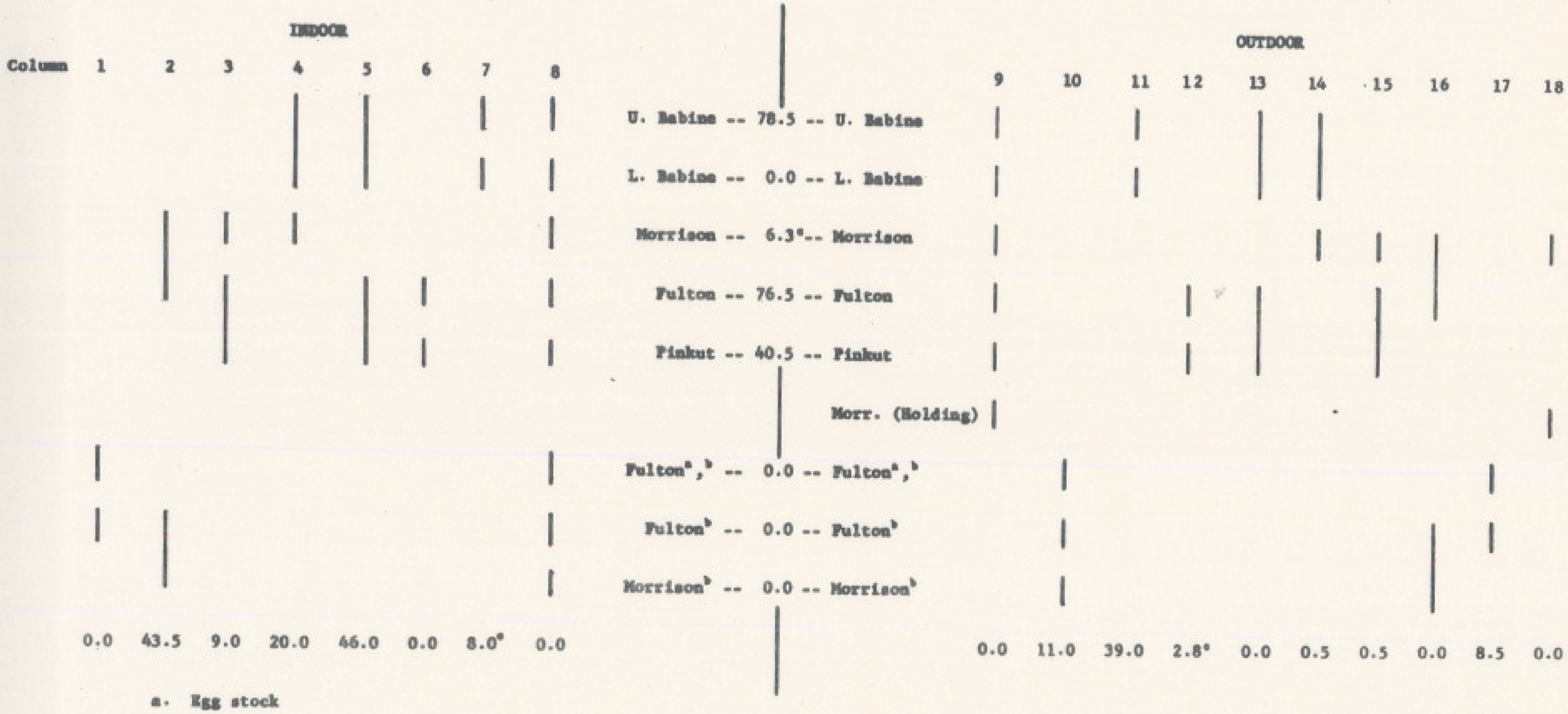
Origin

Similarities between indoor and outdoor results are great enough to suggest a general sequence of consistency in Main Stock origin groups. Pinkut was the most consistent group followed by Morrison, Lower Babine, Upper Babine, and finally Fulton. This trend is also followed by the Z statistics for combined tests (Table 8). Note that Fulton progeny were at least as poorly oriented as progeny from near the outlet while Pinkut River fish, also members of the Main Lake population, had the strongest preferences of all. Morrison was significantly oriented in both test series. However, the Morrison fish which were retested (Holding) were even more consistent and, in fact, were more consistent than any other indoors or outdoors group except the few Pinkut fish tested indoors. These Holding fish had a particularly strong bimodal tendency (Table 8).

To answer the first question, then, both individuals and samples generally had definite preferred directions. This allows examination of the next question.

B. QUESTION 2: DIFFERENCES IN PREFERRED DIRECTIONS

Testing the hypothesis of innate differences depends on finding differences in the preferences of identically reared samples. Figure 11 shows several orthogonal comparisons (Sokal and Rohlf 1969, pp. 458-468) using the randomization test with the B statistic (p. 32). For completeness, it includes data from several Fulton and Morrison "small-tank" stocks which were tested (Appendix C, p. 103). I do not report their analysis elsewhere because they contribute little to solving the problems.



a. Egg stock

b. Raised in small tanks

c. Based on 400 random trials

Fig. 11. Comparisons of directional preferences. Numbers in the central column and along the bottom row are the percent of B statistics from 200 random trials which are greater than B for the actual samples. Samples are assumed to be significantly different if the fraction is less than 5%. Lines indicate the samples which are compared, those joined by lines are pooled together.

1. Indoor tests

Members of the three lake populations, Upper Babine/Lower Babine, Morrison, and Pinkut/Fulton, did not have significantly different directional preferences (Fig. 11, comparisons 3, 4, and 5). Furthermore, Upper Babine and Lower Babine smolts were homogenous as expected, but Pinkut and Fulton were not (comparisons 6 and 7). Indoor groups as a whole were heterogenous (comparison 8), suggesting some innate control. Notwithstanding this overall heterogeneity, the indoor results are evidence against accepting the hypothesis.

The lack of significant differences involving Upper and Lower Babine stocks is due to random distributions in these groups. Morrison and the Pinkut/Fulton composite group were homogenous probably because of true similarities in directions. Morrison preferred an axis, 143-323°, and Pinkut (136°) and Fulton (301°) had a similar distribution when combined.

2. Outdoor tests

Main Stocks tested outside also preferred significantly different directions when considered separately (Fig. 11, comparison 9). Unlike the indoor results, samples of all three lake populations had different directional tendencies as predicted by the hypothesis (comparisons 13, 14, and 15). Since Fulton did not have a significantly strong preference, Pinkut must have strengthened the weak ESE mode of Fulton stock (Fig. 10, p. 41) enough to distinguish the Main Lake preferences from other lake populations. Upper and Lower Babine were similar again (comparison 11) which is also consistent with the hypothesis. In this case, they both had definite preferences so it is concluded that these were in truly indistinguishable directions. Note that Pinkut and Fulton fish were significantly different (P = .0275, 400 trials) despite the almost uniform tendencies of Fulton (comparison 12).

3. Test treatment

Two effects became evident when I examined differences between groups of the same origin. First, Holding smolts oriented in a significantly different direction from their parent Morrison group (Fig. 11, comparison 18) as well as being more consistent in this choice (p. 43). Second, most Main Stocks did not differ in preferences between indoor and outdoor test series (Fig. 11, central figures). Only Lower Babine smolts oriented differently. This general lack of an indoor-outdoor effect is interesting because indoor results were transformed according to an assumed sun-compass mechanism.

To answer the second question, similarities between indoor and outdoor results suggest that a migratory type of orientation may be involved. Furthermore, significant differences between origin groups treated identically strongly suggests that such differences are innate. However, several differences and similarities were unexpected, particularly in the indoor series. This casts doubt on whether migratory orientation was indeed the dominant behavior. This is answered more fully in the next section when adaptiveness of the chosen directions is discussed.

C. QUESTION 3: ADAPTIVENESS OF DIRECTIONAL PREFERENCES

Stocks usually had weak but significant preferences in significantly different directions. How closely do the preferences correspond to migration directions in the lake? Expected migratory directions and those observed (Table 8, p. 40) are:

		Observed	
	Expected	Indoors	Outdoors
Upper Babine	350°	258	82-262**
Lower Babine	350°	165	302**
Fulton	325° → 350°	301**	127-307
Pinkut	325° → 350°	136**	122**
Morrison	155° clockwise → 350°	143-323**	224**

Main Lake and Nilkitkwa Lake populations can migrate in virtually constant directions. The Main Lake smolts shift from 325° to 350° as they enter the North Arm (Fig. 1, p. 3) so I used an average theoretical direction of 335° for this population and 350° for the Nilktkwa stocks.

The four stocks of Main Lake and Nilkitkwa Lake populations usually preferred directions more southerly than expected (above table). Stephen's test (p. 32) was applied to those groups with significantly strong means and circular normal distributions. For the combined tests, this included Fulton, Lower Babine, and Pinkut (Table 8, p. 40). Only Fulton had a central tendency (296°) which was not significantly different ($P > .05$) from the expected migration direction. The Nilkitkwa stocks preferred roughly E-W directions, and Pinkut was strongly oriented to the SE. Pinkut smolts may have been reverse oriented (see Groot 1965) in which case the opposite direction (308°) is quite close to 335°.

This general lack of correspondence between theoretical and observed directions occurred indoors and outdoors. Indoors, Upper and Lower Babine had no directional preferences and Pinkut differed significantly ($P < .01$) from the expected migratory direction (reversed orientation?). Only Fulton smolts responded appropriately (301°). Stephen's test could be used only for Lower Babine and Pinkut groups in the outdoor series. Neither stock preferred a direction significantly close to the theoretical directions. Fulton had no preference in these tests and Upper Babine had bimodal E-W tendencies (82-262°).

Preferences by Morrison smolts had the strongest southerly and easterly component of all groups except Pinkut. These directions are appropriate for migration through Morrison Arm. I calculated mean directions of indoor, outdoor, and combined tests for each week of the season to see if these directions actually occurred at the beginning of the season when the migration would be in Morrison Arm. Fulton, Upper Babine, and Holding groups were analysed in the same way.

I analysed them with linear regression, only using significantly strong means. One week's mean can be reached by shifting either clockwise or anti-clockwise from the mean direction for the previous week. I selected the direction of rotation involving the smallest change. If a bimodal distribution did not have a significant mean, I used the axis direction closest to the preference for the previous week. Trends in circular data can only be distinguished when the residual variation is much less than what would be acceptable in linear situations. The Morrison/indoors group was the only group with an obvious trend (Fig. 12). Fulton/indoors was marginal (Fig. 13) and difficult to interpret.

Based on my criterion for selecting regression points, Fulton smolts oriented about NW throughout the season. Morrison subjects, however, shifted an average of 3.94°/day which is significantly different from 0 ($P < .001$). The shift was clockwise, starting from the south, which is about the expected behavior. They continued to change, however, past north until directions were SE at the end of the experimental period. They preferred NW-N directions in the last half of May, by which time this population is usually out of Babine Lake (Johnson and Groot 1963).

This completes analysis of the three main questions in this study. To summarize results to this point:

(1) Individuals usually oriented strongly.

(2) Variability between individuals was often quite large but most samples had significantly strong preferences.

(3) Preferences were usually significantly different between samples.

(4) The directions preferred did not correspond to those needed to leave Babine Lake in most cases. Morrison was a notable exception in indoor tests.

I discuss possible reasons for these results in the next section by exploring the orientation process.

D. ORIENTATION MECHANISMS

1. Relation between environmental variables and strength of orientation

Strength of orientation by outdoor smolts may be influenced by variation in environmental factors. I used multiple linear regression analysis to assess these coincidental fluctuations and determine the relative importance of each variable. The variables were:

(1) Date

(2) Time of day

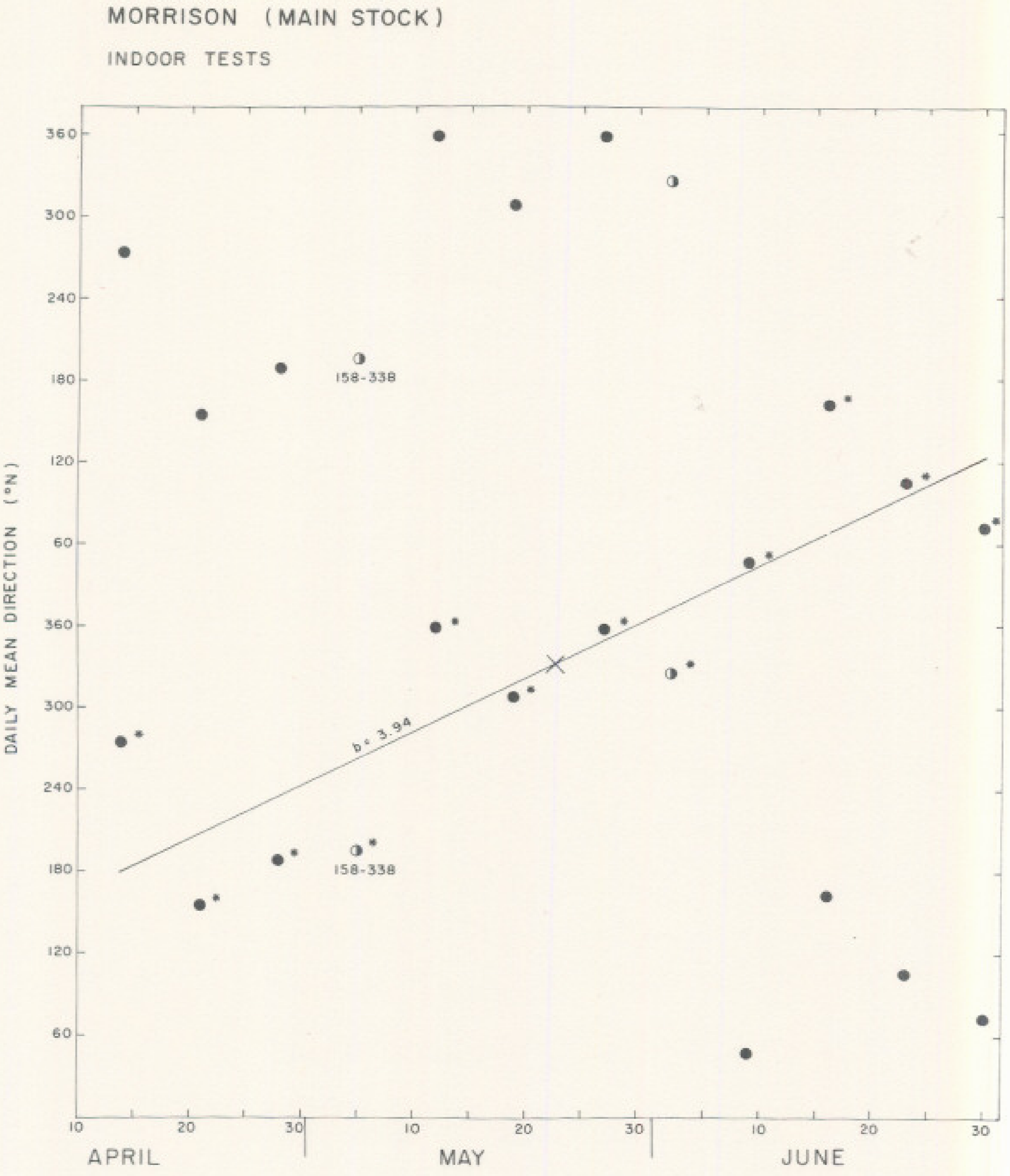


Fig. 12. Preferred directions during the season for indoor tests of Morrison (Main Stock). The least squares regression was calculated from directions marked with asterisks. Note that directions are plotted twice on the vertical axis. Solid circles: unimodal distribution, $P < 1\%$, half-solid: $5\% > P > 1\%$. Significantly strong bimodal distributions are shown by dotted symbols when the unimodal mean direction is insignificant. The mean direction for May 5 shows a bimodal axis as well because the mean is barely significant at the 5% level.

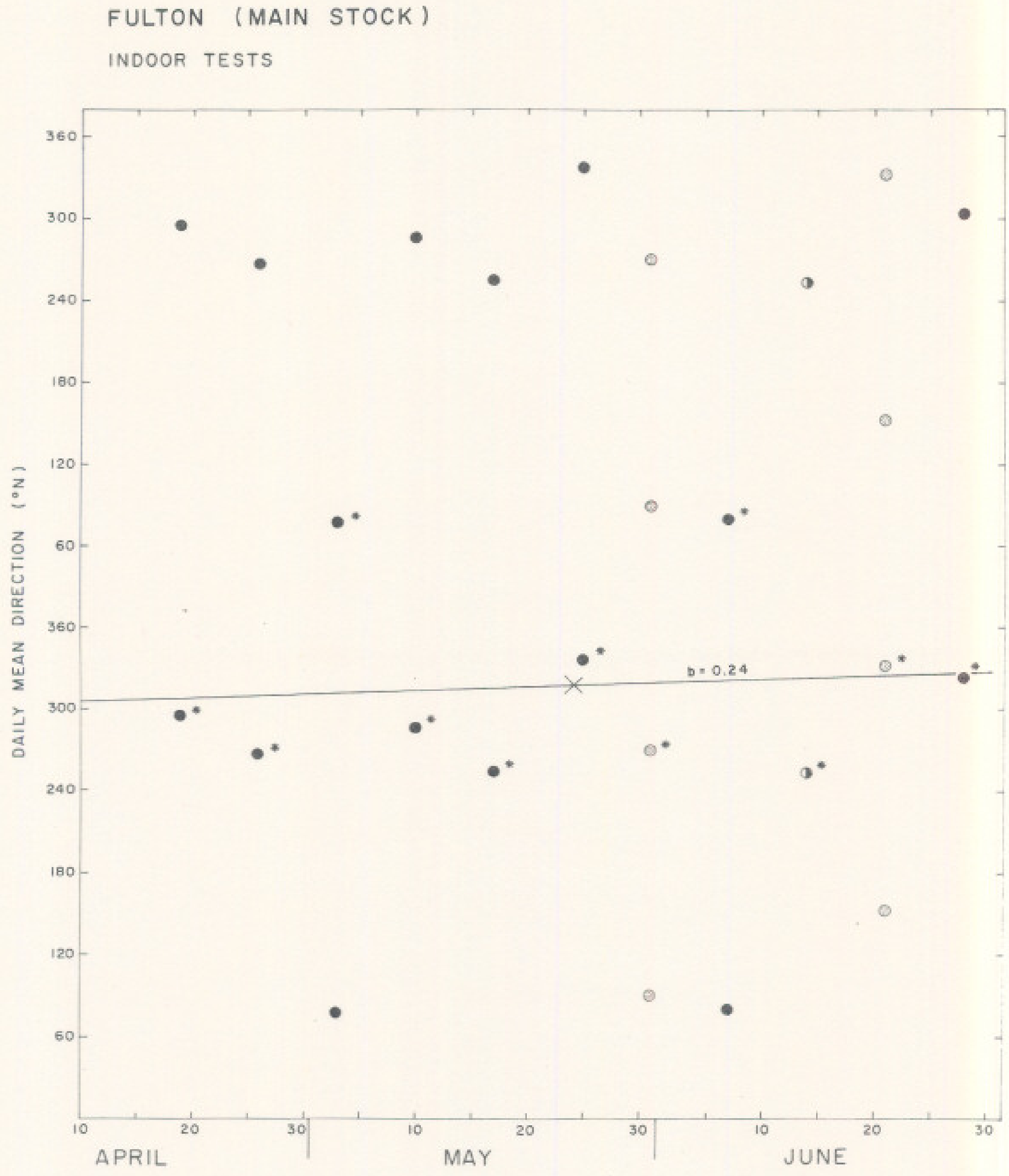


Fig. 13. Preferred directions during the season for indoor tests of Fulton (Main Stock). See Fig. 12 (p. 51) for details.

(3) Light intensity[4]

(4) Radiation[4]

(5) Air temperature[4]

(6) Water temperature[4]

(7) Cloud cover[4]

(8) Sun visibility[4]

(9) Moon visibility[4]

(10) Wind velocity[4].

Significant variables can be selected by multiple regression in several ways and the methods may produce different solutions. I used two computer programs: the IBM 1130 Statistical System stepwise regression package and a backward elimination regression program (Lindsey 1971). These opposite analytical approaches (see Draper and Smith 1966) produced virtually identical results. Of the ten variables, only sun visibility "explained" a significant amount of the variability in $\bar{a}$. The stepwise regression equation is:

$$\bar{a} = 0.531 + 0.027 \text{ (Sun visibility)}$$

where sun visibility ranges from 0 (invisible) to 4 (bright). This linear model adequately explains the observations since the lack of fit mean square is not significant. The regression coefficient is significantly different from 0 ($P < .001$). Despite this, however, only 3.2% of the variance in $\bar{a}$ is accounted for. The residual variance is reduced very slightly with the addition of moon visibility but its regression coefficient is not significantly different from 0. I confirmed this relationship by calculating the mean $\bar{a}$'s for each test session (usually three subjects/session) and regressing these on sun visibility (Fig. 14).

2. Constant angle orientation

Either sun-compass orientation or orientation at constant angles to the light source could explain why orientation strength increased with better sun visibility. I examined this in indoor and outdoor tests by referring all pointings to the light source so that 0° was the lamp or sun direction. Table 9 shows that transformed pointings were generally more concentrated, i.e., new Rayleigh statistics, Z, generally exceeded original values. Ignoring bimodal distributions[5], differences were:

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[4] See Table 3, p. 24.

[5] Z values are only rough indicators of dispersion in bimodal distributions.

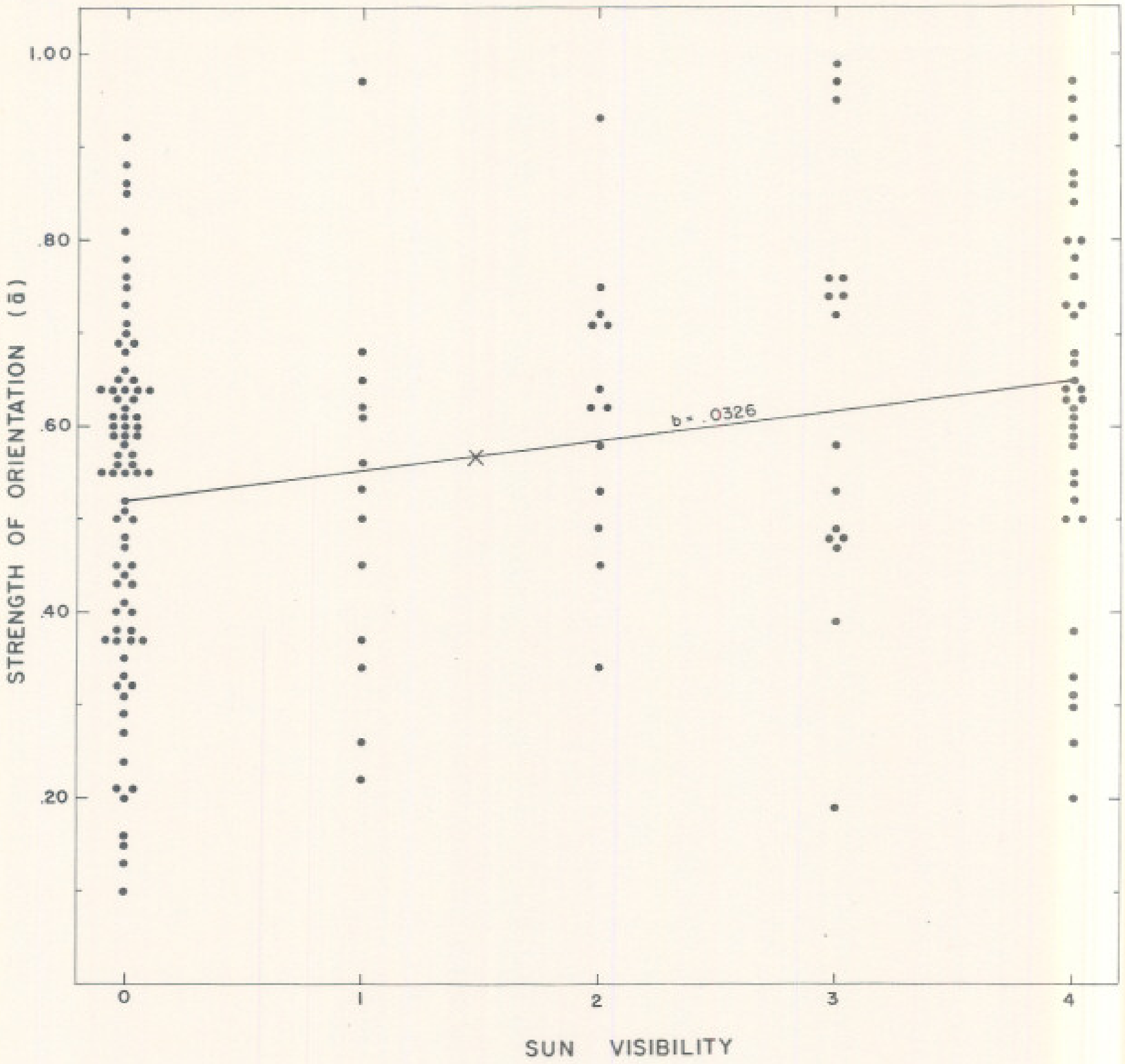

Fig. 14. Change in strength of orientation with sun visibility. $\bar{a}$ values are means of the $\bar{a}$'s for all subjects in one test session (usually three/session). Sun visibility was rated on a 0-4 scale from invisible to fully bright.

Table 9. Summary of orientation relative to the light source by Main Stocks.

	Indoor tests						Outdoor tests					
	Lamp azimuth = Sun azimuth			Lamp azimuth = 0°			North = 0°			Sun azimuth = 0°		
Origin	Mean	$\bar{a}$	Z	Mean	$\bar{a}$	Z	Mean	$\bar{a}$	Z	Mean	$\bar{a}$	Z
Fulton	301	.11	7.19**	27	.17	17.34**	283	.02	0.42	344^a	.06	4.99**
							127-307	.03	1.14	91-271	.08	11.13**
Upper Babine	258	.06	2.60	352^a	.09	5.01**	222	.01	0.05	267	.02	0.45
				159-339	.16	16.48**	82-262	.07	6.38**	8-188	.10	12.78**
Morrison	198	.09	5.13**	347^a	.10	7.12**	224	.08	11.08**	11^a	.09	13.65**
	143-323	.13	10.98**									
Lower Babine	165	.16	2.76	252	.11	1.42	302	.20	17.54**	89	.23	22.31**
				19-199	.24	6.45**				73-253	.28	32.29**
Pinkut	136	.53	22.86**	340^a	.23	4.37*	122	.18	11.62**	301	.26	24.27**
				153-333	.46	17.30**						
Morrison (Holding)							55	.10	13.48**	282	.04	2.45
							64-244	.16	32.82**	121-301	.17	34.94**

^{a}Mean is not significantly different from 0° ($P < .05$).

	Indoor	Outdoor
	(New Z - original Z)	(New Z - original Z)
Fulton	+10.15	+4.57
Upper Babine	+2.41	+0.40
Morrison	+1.99	+2.57
Lower Babine	-1.34	+4.77
Pinkut	-18.49	+12.65
Mean	-1.06	+4.99

The small Pinkut sample (six tests) is largely responsible for the mean decrease indoors. Excluding Pinkut, Z increased an average of 3.3 units.

The stronger orientation relative to the light source means that constant angle orientation (C.A.O.) was an important component in indoor and outdoor results. It almost certainly was a reaction to the sun in outdoor tests because smolts must have followed the sun, changing pointing directions with changes in sun azimuth. The lamp or any other stationary cue could have been used indoors, although outdoor results support an hypothesis that the lamp was the cue.

3. Directions relative to the light source

Indoor tests

Directions relative to the lamp (Table 9, p. 59) were examined to see if it was the cue. Smolts oriented either towards the lamp (Fulton and Morrison) or towards and away from it (Upper and Lower Babine and Pinkut). The mode towards the lamp was strongest in Upper Babine and Pinkut samples. These results suggest that phototaxis, particularly positive phototaxis, was the C.A.O. mechanism indoors.

Phototaxis is particularly evident when pointings by Major Stocks are examined at each test time (Table 10). Angles between the lamp and the nearest mode of pointings averaged 11°, 25.3°, and 59° at noon, 16:00, and dusk. Opposite modes occurred at noon, while all subjects oriented toward the lamp at 16:00. Stronger unimodal preferences near the lamp in afternoon tests explain why variation within Major Stocks was least at this time (p. 38). Comparison of dispersions (Z statistics) before and after making the lamp direction equal to 0° shows that C.A.O. was strongest at 16:00 and weakest at dusk. In fact, Z at dusk always decreased after transformation.

Pinkut and Morrison groups seem to be least prone to C.A.O. indoors (Table 9, p. 59). Recall, that the Morrison group also shifted directions in approximately the expected manner during the season.

Table 10. Directional preferences of the Major Samples at each test time.

	Noon	Afternoon	Dusk
Mean sun azimuth	171	253	295
<u>Indoor tests</u>			
Fulton	169-349**[a]	287*	325**
Upper Babine	168-348*	260**	91-271**
Morrison	143**	288**	172**
<u>Outdoor tests</u>			
Fulton	86-266**	2-182**	318*
Upper Babine	14-194**	93-273**	85-265**
Morrison	208**	236**	32-212*

[a] Bimodality is indicated when the doubled angles give a significant mean vector (as shown by asterisks) but the actual mean vector is not significant.

Outdoor tests

Examination of outdoor preferences relative to the sun (right column of Table 9, p. 59) shows that only Morrison and Upper Babine had phototaxis-like preferences. The rest oriented 60 to 90° from the sun/anti-sun axis. Of the transverse orientations, only Pinkut's was unimodal. Generally, different mechanisms appear to be operating in indoor and outdoor tests.

Table 10 (p. 61) shows that Major Stocks preferred directions averaging 48°, 36°, and 45° from the sun azimuth at noon, 16:00, and dusk, respectively. Outdoor preferences relative to the sun changed little between test times while indoor values increased with time of day (11°, 25.3°, and 59°).

However, analysis of dispersions for outdoor tests shows the same pattern as indoors, i.e., C.A.O. strongest at 16:00 and weakest at dusk. Major Stocks tested at dusk oriented better relative to north than to the sun azimuth, like in indoor tests.

4. Summary

(1) Individuals oriented more strongly with increased sun visibility.

(2) Constant angle orientation predominated over sun-compass orientation except in Morrison and possibly Pinkut indoor smolts.

(3) C.A.O. was strongest at 16:00 and weakest at dusk, indoors and outdoors. There were fewer bimodal responses at 16:00.

(4) Indoor smolts generally pointed towards the light and outdoor Main Stocks usually had transverse orientations, averaging 43° from the sun.

(5) The mechanisms used appear to be different in indoor and outdoor tests although both are related to the light source. Phototaxis is the probable mechanism indoors.

DISCUSSION

The objective of this study was to look for innate orientation differences between the three smolt populations in Babine Lake. To summarize 1970 (Appendix A, p. 75) and 1971 results:

Did subjects have directional tendencies? Individuals from all streams usually oriented strongly when tested in small drum tanks. Preferences in each sample were usually diverse but not random, i.e., most stocks had significant preferences. Morrison was most strongly oriented in both years.

Did samples have different directional tendencies? Several significant differences occurred and I concluded that these were innate.

Did directional tendencies correspond to migration directions in the lake? They did not correspond in most samples.

These results largely arose because smolts oriented at constant angles to the light source. Two likely explanations are that (1) subjects responded to the light source as a cue, or (2) they preferred tank areas with certain light intensities, the locations of which depended on the position of the light source. The first possibility seems most probable in indoor tests because the transparent drum tanks seemed to be uniformly illuminated. Smolts usually oriented toward or away from the lamp, strongly suggesting that they were weakly phototactic. Past studies on Oncorhynchus light responses (Fields and Finger 1954a, b; Hoar 1954, 1955, 1958; Hoar, Keenleyside, and Goodall 1957) measured light intensity preferences and not phototaxis in its proper sense (see p. 5).

Other animals often orient phototactically when raised or tested without view of the sky (e.g. Arthropods: Lindauer 1959, Pardi 1960, Papi and Tongiorgi 1963; fish: Schwassmann 1962; birds: Hoffmann 1960, Merkel 1971). Most workers describe this behavior as an artifact because, although it occurs under more natural conditions (e.g. Pardi 1960; Brown and Mewaldt 1968), it is not as frequent.

The outdoor series was such a "natural" test situation and was actually undertaken partly as insurance in case constant angle orientation predominated indoors. Unfortunately, the films show that smolts preferred shadows in the painted drums. I suggest that this affected their orientation, masking any true phototaxis or other mechanism. Photonegativity explains several outdoor results:

(1) Variability between successive pointings was less outdoors (Appendix B, p. 93). Smolts often kept their head near the shaded wall by lying against it or pointing towards it. Thus, the wall restrained their orientation.

(2) Individual orientation strengths weakened from noon to dusk and with reduced sun visibility. About half of the drum tank volume was illuminated at noon in sunny weather, one side of the wall was illuminated at 16:00, and the whole tank was in shade at dusk. Other orientation mechanisms did not become manifest when photonegative responses were reduced under cloudy skies and at dusk.

(3) Bimodal preferences were common. I observed that smolts not only preferred darker tank areas but they often returned to the same wall area. Lying against the same wall causes opposite orientations depending on whether its right or left side is next to the wall.

(4) Most bimodal axes were transverse to the sun/anti-sun axis, some about 90° to it. The wall area in deepest shade, and thus most preferred, was that part nearest the sun and perpendicular to its azimuth.

(5) Smolts rarely preferred directions opposite to the sun for the same reason as in (4).

I conclude that orientation by outdoor smolts was largely, perhaps entirely, due to avoidance of brighter areas in the tank. Groot (1965) had a similar problem in his noon and afternoon tests of Nilkitkwa Lake smolts.

What were the problems? Three possibilities are: (1) these populations do not have innate differences with respect to migration directions, (2) this study's hypothesis is correct and my smolts had functional migratory orientation mechanisms, but raising and testing disturbances blocked their expression, and (3) proper mechanisms were absent because certain experiential factors, necessary for their development, were lacking.

Morrison and Main Lake populations almost certainly do not leave their respective nursery areas in significant numbers until the smolt stage (Johnson 1958; Johnson and Groot 1963; McDonald 1969; Scarsbrook and McDonald 1970, 1972), i.e., they could not learn the routes. Possibility (1) means, therefore, that there are different environmental influences in each lake population that cause smolts to travel in specific directions toward the outlet. The most likely environmental factor would be lake currents but the outlet flow is very small for a lake of this size and measurements indicate that currents mainly depend on wind (Johnson and Groot 1963; D. Farmer, personal communication) and are not related to the outlet direction. Most important, Groot (1965) observed adaptive directional preferences in these populations even when smolts were held and retested throughout the season. They shifted preferences roughly as they would if they were actually travelling the route, strongly suggesting that my hypothesis is correct.

Considering the second possibility of indirect disturbances, there is some evidence that smolts were under considerable stress during tests. Films show that smolts often fluttered, especially in indoor tests. This behavior consists of intense swimming activity in which the smolt flutters against the sides and bottom of the tank and makes sudden, erratic turns. It has been considered as migratory behavior (Iersel 1953; Groot 1965) and as escape behavior (Hoar 1954; Hoar et al. 1957) and is probably a combination of both (Ellis 1964). The clear tank walls and uniform illumination provided less cover indoors, increasing this stress-indicating behavior. Lack of cover was probably the reason indoor smolts clustered pointings less and were more active than outdoors (Appendix B, p. 93). The cover-seeking response is very strong in other fish and has been used in orientation training experiments (Hasler et al. 1958; Hasler and Schwassmann 1960; others reviewed by Hasler 1971).

Numerous field observations point to negative light reactions in juvenile sockeye. Babine Lake underyearlings are deep (20-40 m) during the day and only surface for brief periods at dusk and dawn (Narver 1970). Narver's echo sounding and fishing studies show that they go deeper with advancing season. Recent work suggests that, by the following spring, most Main Lake smolts are 50-60 m deep during the day and do not rise above 20 m at night (Simpson, Turner, and Groot, unpublished). Some smolts occur near the surface but only at dusk and dawn (Johnson and Groot 1963). Apparently, juvenile sockeye live in almost complete darkness most of the time and probably never occur in more than twilight conditions, even when migrating.

The outdoor results and several other laboratory studies confirm that sockeye are photonegative up to and including at least the smolt stage (Fields and Finger 1954a, b; Hoar 1954, 1955, 1958; Hoar, Keenleyside, Goodall 1957). Light levels during raising and testing were therefore higher than in natural conditions.

I have already suggested how light intensities during the tests produced artifacts. Light intensities were much lower in the raising tanks but still greater than would normally be experienced. Raising conditions did not prevent onset of smoltification with its attendant increase in activity or "migratory restlessness." Even so, it is possible that raising conditions, especially light levels and possibly crowding effects, were a disturbing factor.

The third possibility is that raising conditions may have lacked specific environmental factors necessary for development of orientation mechanisms. Despite similar testing techniques, Groot (1965) found that smolts caught and tested on Babine Lake generally oriented adaptively. I assumed that normal development of an orientation ability could occur without experiencing celestial cues. Several other species can orient using artificial or actual celestial cues on their first exposure to them (Birukow 1956 [water skater, Velia]; Pardi 1960 [littoral amphipods: Talitrus, Talorchestia, and Orchestia]; Papi and Tongiorgi 1963 [wolf spider, Arctosa]; Hoffmann 1953 [starling, Sturnus]; Sauer 1957 [garden and blackcap warblers, Sylvia]; Braemer 1960 and Schwassmann 1962 [green sunfish, Lepomis]).

There are also examples where experiential factors are necessary, however. Emlen (1969, 1970) has evidence that Indigo Buntings (Passerina) must learn to use the stars to orient at night. They apparently sense the nightly rotation of stars around Polaris and learn to associate stellar patterns with the axis of rotation. Immature Parrot fishes (Scarus) did not use sun-compass orientation in shore areas of Bermuda, whereas adults clearly did (Winn, Salmon, and Roberts 1964). The authors suggest that the sun-compass mechanism is learned in this species. Wallraff (1966) found that homing in pigeons was affected if he blocked various views of the horizon during raising. Sockeye orientation may also require some experience with natural cues. If so, the experience given to Holding smolts was not sufficient.

Whatever the experimental inadequacies, they did not completely prevent migratory orientation in Morrison and perhaps Pinkut smolts. Morrison subjects were least prone in all test situations to constant angle orientation and in one, 1971 indoors, they oriented as expected. This required compensating for imaginary sun movements, strongly suggesting that they used a sun-compass mechanism.

The shift of 3.94°/day in the 1971 Morrison indoors group compares favorably with Groot's (1965) observations. Smolts tested as they migrated down Morrison River ("run-sample") shifted 5.6°/day in 1961 and 3.8°/day in 1962; smolts subsequently caught in the North Arm and at the outlet probably shifted from 6.0° to 7.4°/day. My subjects were already oriented S at the beginning of tests in mid-April, whereas naturally migrating fish did not head S until late May-early June. By the end of tests on June 19-20, run-sample smolts were oriented W to NW, but mine had already shifted around to E. Groot's smolts were shifting just as rapidly at the end of his tests, suggesting that they too continued past N, the direction of the lake outlet. Virtually all of the Morrison population would be out of the lake by this time so it probably is not harmful.

Earlier timing of the hatchery smolts may mean that they were ontogenetically more advanced. Their activity, interpreted as migratory restlessness, also increased some time before the normal migration period in May. My smolts were raised in warmer water during the two winters.

Morrison is the most unique group, but other samples also consistently differed in their susceptibility to constant-angle orientation. In general, however, preferred directions are related to phototaxis and photonegativity. This makes analysis difficult because the results depend on the particular test situation: most stocks changed preferences between years.

This study has shown that stream populations were innately different in responses to a given test situation but it neither proves nor disproves the hypothesis that Babine stocks have genetically distinct migratory orientations. Future laboratory studies of this nature may be more conclusive if the following were done:

(1) Raise smolts in large outdoor tanks. The tanks should be covered to reduce light intensities while allowing at least a partial view of the sky.

(2) Test smolts in near or complete darkness.

(3) Perhaps eliminate as many visual cues as possible. Laboratory studies at Babine Lake showed that smolts can orient in expected directions under these conditions (Groot 1965). Their preferred depths in the lake would appear to make this capacity obligatory.

(4) Once migratory orientation is obtained, cross-breeding experiments can be used to examine the genetic component in more detail.

Artifacts due to raising and/or testing conditions are a major problem with this type of study. Perhaps it is not surprising, therefore, that few studies have tried to demonstrate innate behavior differences within a species. Most deal with interracial differences (e.g. Boch 1957; Pittendrigh 1958; Rothenbuhler 1964; Grossfield 1971). Very few have looked at geographic variation within a taxonomically "uniform" group (e.g. Dix 1968).

Salmonids are a particularly good family to make this kind of study on because many, particularly the anadromous species, have very strong and precise homing tendencies. This allows an exceptional amount of intraspecific genetic diversity to occur between local populations. Indeed, differences between stocks of Pacific salmon have been recognized for some time (reviewed by Ricker 1972). Calaprice (personal communication) has shown that the stream populations in this study are genetically different. He reared parental and hybrid progeny under similar, controlled conditions and found differences in all characters examined: survival, growth rates, and rheotaxis. Rheotaxis differences in fry depended on whether they came from the outlet, i.e., whether their population has to swim against or with the current to reach the nursery lake. Similar rheotaxis studies have been made by Brannon (1967, 1972), Raleigh (1967, 1971) and Kelso (1972).

Considering its basic importance to management policies, however, there is surprisingly little known about genetic diversity in salmonids. As Behnke (1972) stresses:

> "It has been much simpler and more expedient to assume that the striking differences in behavior and life histories between stocks within a species are only nongenetic expressions of direct environmental influence. Critical research to delineate the genetic and environmental factors determining the life history differences have lagged. Hopefully, the fact that accurate knowledge of the genetic basis of behavior is of major importance for effective management of a species will be more generally recognized by fisheries scientists and administrators."

SUMMARY AND CONCLUSIONS

My hypothesis that each Babine Lake population has innately different directional preferences was tested by raising samples in the same environment. An efficient analysis procedure, based on finding when directions become independent, allowed a large amount of data to be collected.

Individuals usually oriented strongly when tested in small drum tanks. Indoor orientations were stronger than those outdoors and this strength increased as the season progressed. Orientation strengths did not change with time of day in indoor tests but declined from noon to dusk outside. Looking at group orientations, preferences of the individuals in each stream group were quite variable but usually non-random. Bimodal preferences were common, particularly in outdoor tests. Morrison and Pinkut groups were the most strongly oriented of the groups and retesting increased the consistency of Morrison preferences even more.

Group preferences were generally indistinguishable between indoor and outdoor test series while significant differences in directional preferences occurred between origin groups. These results indicate innate differences as hypothesized but several differences and similarities were unexpected. Indeed there was little correspondence between the directions preferred and those expected from knowledge of the migration routes. Morrison smolts tested indoors were a notable exception, where the expected seasonal shift occurred.

It seems likely that smolts other than Morrison and possibly Pinkut groups used orientation mechanisms different from those used in lake migration. Furthermore, the mechanisms probably differed between indoor and outdoor test series. I concluded that phototaxis predominated indoors and photonegativity, seeking shade, was the primary outdoor response.

Raising and testing conditions, both involving light intensities greater than would normally be experienced, probably (a) disturbed the animals, reducing their motivation for this behavior, and/or (b) lacked certain experiential factors necessary for development of a migratory orientation ability. I suggest that this is a more likely explanation of the results than the alternative that the hypothesis is incorrect. The study substantiates this insofar as (a) Morrison smolts responded appropriately indoors, and (b) innate differences were found in orientation responses to the test conditions.

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REFERENCES

Adler, H. E. 1970. Ontogeny and phylogeny of orientation, p. 303-336. In L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt [ed.] Development and evolution of behavior. W. H. Freeman and Co., San Francisco.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S. Monograph, Washington, D.C. 57 p.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. 29: 639-671.

Birukow, G. 1956. Lichtkompassorientierung beim wasserläufer *Velia currens* F. (Heteroptera) am tage und zur nachtzeit. I: Herbst-und winterversuche. Z. Tierpsychol. 13: 463-484.

Boch, R. 1957. Rassenmässige unterschiede bei den tänzen der honigbiene (*Apis mellifica* L.). Z. Vgl. Physiol. 40: 289-320.

Braemer, W. 1960. A critical review of the sun-azimuth hypothesis. Cold Spr. Harb. Symp. Quant. Biol. 25: 413-427.

Bram, J. 1970. A computer program for unbalanced analysis of variance. Center for Naval Anal. Res. Contrib. No. 164. Technical Information Service, U.S. Dep. Commerce, Washington, D.C.

Brannon, E. L. 1967. Genetic control of migrating behavior of newly emerged sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Prog. Rep. 16: 31 p.

1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. XXI: 86 p.

Brown, I. L., and L. R. Mewaldt. 1968. Behavior of sparrows of the genus *Zonotrichia*, in orientation cages during the lunar cycle. Z. Tierpsychol. 25: 668-700.

Dix, M. W. 1968. Snake food preference: innate intraspecific geographic variation. Science 159: 1478-1479.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, New York. 407 p.

Ellis, D. V. 1964. Experiments on the effect of captivity on salmon behavior. Fish. Res. Board Can. MS Rep. 756: 32 p.

Emlen, S. T. 1969. The development of migratory orientation in young indigo buntings. The Living Bird 8: 113-126.

1970. Celestial rotation: its importance in the development of migratory orientation. Science 170: 1198-1201.

Fields, P. E., and G. L. Finger. 1954a. The reaction of young Salmonidae to light. Univ. Wash. School Fish. Tech. Rep. 2: 20 p.

1954b. The reaction of five species of young Pacific salmon and steelhead trout to light. Univ. Wash. School Fish. Tech. Rep. 7: 24 p.

Fraenkel, G. S., and D. L. Gunn. 1961. The orientation of animals. Dover Publications, New York. 376 p.

Goodyear, C. P. 1970. Terrestrial and aquatic orientation in the starhead topminnow, *Fundulus notti*. Science 168: 603-605.

Goodyear, C. P., and D. E. Ferguson. 1969. Sun-compass orientation in the mosquito-fish, *Gambusia affinis*. Anim. Behav. 17: 636-640.

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.

Groot, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behav. (Suppl.) XIV: 198 p.

1972. Migration of yearling sockeye salmon (*Oncorhynchus nerka*) as determined by time-lapse photography of sonar observations. J. Fish. Res. Board Can. 29: 1431-1444.

Grossfield, J. 1971. Behavioral differentiation of three races of *Drosophila auroria*. J. Hered. 62: 117-118.

Hamilton, W. J. 1966. Analysis of bird navigation experiments, p. 147-178. *In* K. Watt [ed.] Systems analysis in ecology. Academic Press, New York.

Harden Jones, F. R. 1968. Fish migration. Edward Arnold (Publishers) Ltd., London. 325 p.

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

1971. Orientation and fish migration, p. 429-510. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. VI: Environmental relations and behavior. Academic Press, New York.

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

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

Healey, M. C. 1967. Orientation of pink salmon (*Oncorhynchus gorbuscha*) during early marine migration from Bella Coola River system. J. Fish. Res. Board Can. 24: 2321-2338.

Hoar, W. S. 1954. The behaviour of juvenile pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 11: 69-97.

1955. Phototactic and pigmentary responses of sockeye salmon smolts following injury to the pineal organ. J. Fish. Res. Board Can. 12: 178-185.

1958. The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. J. Fish. Res. Board Can. 15: 391-428.

Hoar, W. S., M. H. A. Keenleyside, and R. G. Goodall. 1957. Reactions of juvenile Pacific salmon to light. J. Fish. Res. Board Can. 14: 815-830.

Hoffmann, K. 1953. Die einrechnung der sonnenwanderung bei der richtungsweisung des sonnenlos aufgezogenen Stares. Naturwiss. 40: 148.

1960. Experimental manipulation of the orientational clock in birds. Cold Spr. Harb. Symp. Quant. Biol. 25: 379-387.

Iersel, J. J. A. van. 1953. An analysis of the parental behaviour of the male three-spine stickleback (Gasterosteus aculeatus L.). Behav. (Suppl.) III: 159 p.

Johnson, W. E. 1956. On the distribution of young sockeye salmon (Oncorhynchus nerka) in Babine and Nilkitkwa Lakes, B.C. J. Fish. Res. Board Can. 13: 695-708.

1958. Density and distribution of young sockeye salmon (Oncorhynchus nerka) throughout a multibasin lake system. J. Fish. Res. Board Can. 15: 961-982.

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. Board Can. 20: 919-938.

Kelso, B. 1972. Genetic and environmental mechanisms controlling the lakeward migration of young rainbow trout (Salmo gairdneri) in outlet and inlet streams of Loon Lake and Pennask Lake, British Columbia. MS Univ. British Columbia, Vancouver, B.C.

Kramer, G. 1952. Experiments on bird orientation. Ibis 94: 265-285.

Krumbein, W. C. 1939. Preferred orientation of pebbles in sedimentary deposits. J. Geol. 47: 673-706.

Landreth, H. F., and D. E. Ferguson. 1968. The sun-compass of fowler's toad, Bufo woodhousei fowleri. Behav. 30: 27-43.

Lindauer, M. 1959. Angeborene und erlernte komponenten in der sonnenorientierung der bienen. Z. ugl. Physiol. 42: 43-62.

Lindsey, J. K. 1971. Programs for multiple regression and analysis of covariance. Fish. Res. Board Can. Tech. Rep. 276: 17 p.

McDonald, J. G. 1969. Distribution, growth, and survival of sockeye fry (Oncorhynchus nerka) produced in natural and artificial stream environments. J. Fish. Res. Board Can. 26: 229-267.

Marler, P., and W. J. Hamilton. 1966. Mechanisms of animal behavior. John Wiley and Sons, New York. 771 p.

Merkel, F. W. 1971. Orientation behavior of birds in Kramer cages under different physical cues. In H. E. Adler [ed.] Orientation: sensory basis. Ann. N.Y. Acad. Sci. 188: 283-294.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27: 281-316.

Papi, F., and P. Tongiorgi. 1963. Innate and learned components in the astronomical orientation of wolf spiders. Ergeb. Biol. 26: 259-280.

Pardi, L. 1960. Innate components in the solar orientation of littoral amphipods. Cold Spr. Harb. Symp. Quant. Biol. 25: 395-401.

Pittendrigh, C. S. 1958. Adaptation, natural selection, and behavior, p. 390-416. In A. Roe and G. G. Simpson [ed.] Behavior and evolution. Yale Univ. Press, New Haven.

Raleigh, R. F. 1967. Genetic control in the lakeward migrations of sockeye salmon (Oncorhynchus nerka) fry. J. Fish. Res. Board Can. 24: 2613-2622.

1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. Ecology 52: 291-297.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations, p. 19-160. In R. C. Simon and P. A. Larkin [ed.] The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.

Rothenbuhler, W. C. 1964. Behavior genetics of nest-cleaning in honey bees. IV: Responses of F_1 and backcross generations to disease-killed brood. Am. Zool. 4: 111-123.

Sauer, E. F. G. 1957. Die sternenorientierung nächtlich ziehender grasmücken (Sylvia atricapilla, borin, und curruca). Z. Tierpsychol. 14: 29-70.

Scarsbrook, J. R., and J. G. McDonald 1970. Purse seine catches of sockeye salmon (Oncorhynchus nerka) and other species of fish at Babine Lake, British Columbia, 1966 to 1968. Fish. Res. Board Can. MS Rep. 1075: 110 p.

1972. Purse seine catches of sockeye salmon (Oncorhynchus nerka) and other species of fish at Babine Lake, British Columbia, 1971. Fish. Res. Board Can. MS Rep. 1189: 48 p.

Schwassmann, H. O. 1960. Environmental cues in the orientation rhythm of fish. Cold Spr. Harb. Symp. Quant. Biol. 25: 443-449.

1962. Experiments on sun orientation in some freshwater fish. Ph.D. Thesis. Univ. Wisconsin. 153 p. Univ. Microfilms. Ann Arbor, Mich.

Simpson, K. S., and C. Groot. 1972. Programs for analysis of orientation data. Fish. Res. Board Can. Tech. Rep. 312: 61 p.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.

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

U.S. Navy Hydrographic Office. 1952. Tables of computed altitude and azimuth. H.O. Pub. No. 214. U.S. Government Printing Office, Washington, D.C. 9 vol.

Wallraff, H. G. 1966. Über die heimfindeleistungen von brieftauben nach haltung in verschiedenartig abgeschirmten volieren. Z. Vgl. Physiol. 52: 215-259.

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

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

APPENDIX A

1970 EXPERIMENTS

Preliminary tests were run in 1970 on a different collection of fish. I tested them in several ways, attempting to find an acceptable technique. This made analysis of results more difficult but 1971 data can be examined in better perspective with an additional year's results.

MATERIALS AND METHODS

A. EXPERIMENTAL ANIMALS

1. Collection

I obtained samples for 1970 tests in November, 1969. The fingerlings had been collected as eggs and alevins on March 20, 1969 from Upper and Lower Babine rivers, the Morrison system, and Fulton River. There were about 160, 200, 26, and 75 from each respective stream. Collection procedures were virtually identical to those already discussed (p. 5).

2. Raising

Salmon were all raised in the small tanks at Rosewall Hatchery (p. 5) under approximately natural photoperiods.

3. Holding

Smolts were transported weekly between the hatchery and the Pacific Biological Station as in 1971. Each of the four stocks were held in 35-ℓ glass aquaria, with a continuous water flow. The aquaria stood in a water bath of a large refrigerated tank (2.5 × .91 × .86 m) with temperatures fairly close to those at Rosewall (about 9 C). Three 40-W lights were turned on and off at sunrise and sunset by clock-control. Smolts were fed Oregon Moist Pellet commercial food once a day but most did not feed.

B. EXPERIMENTAL PROCEDURE

I ran tests in the basement of the Biological Station at 12:00, 16:00, and sunset for 4 days a week from April 13 to June 30. Morrison smolts were tested on Monday, Upper Babine on Tuesday, Lower Babine on Wednesday, and Fulton on Thursday. Only indoor tests were done, using one naive fish in each test (Table 1, p. 6).

1. Apparatus

The orientation stand was identical to that used in 1971 outdoor tests (p. 9). Smolts were tested in the large tank (84 cm diameter, 23 cm high) which acted as the reservoir in 1971. A small painted drum tank (30 cm diameter), placed in the center of the large tank, was used after June 9. Room features were blocked out by draping a linen sheet over the metal shields around the tank. The "sun" was originally a 750-W flood lamp attached to a pole so it remained 2.9 m and about 50° elevation from the center of the tank. This whole arrangement was altered several times in an effort to elicit stronger and more appropriate responses in the subjects (see Table 11).

The smolt was monitored with a television camera (Sony DXC-2000A), the lens of which projected through a plastic screen under the orientation tank (as in Fig. 2, p. 11). The picture was recorded on video tape (Sony Videocorder EV-310; Sony Video Tape V-11-60).

2. Procedure

The orientation tank was filled to a depth of 13 cm with water at the holding tank temperature. After introducing the fish, the tank was carefully covered with the sheet so no folds were visible and the lamp turned on. The video picture was recorded on tape for 15 min after a 2-hr adaptation period. By the end of the test, water temperatures had risen 2 to 4°.[6]

C. DIRECTIONAL MEASUREMENTS

Directions were measured in two ways. The main method was to record the direction of the smolt's body axis every 3 sec using the Trilateral Reader and a television monitor (Trilateral method). Head and tail positions were obtained with a light-beam pointer which eliminated parallax problems on the curved screen. This is very similar to the 1971 method except measurements were taken regardless of the animal's motion.

Directions of smolts while stationary were also recorded during the test from the monitor in the adjoining room (pointings method). The picture of the tank was divided into 16 sectors. I recorded a frequency distribution of pointings for each test by estimating which sector included the smolt's direction whenever it remained still for 3 sec. This is identical to Groot's method "f" (Groot 1965, p. 29-30) so it provided a basis for comparison.

RESULTS

Test results (Appendix C, p. 103) were examined in relation to:

(1) test time,

(2) test procedure,

(3) origin of samples.

---

[6] Cold water was circulated through a bottom compartment in the tank in preliminary experiments but cooling was insufficient and it produced large fields of bubbles on the false bottom.

Table 11. Changes in testing situation during 1970 season.

Treatment number	Date	Test numbers	Description
1	Apr. 13-16	1-11	Initial arrangement
2	Apr. 27-May 7	12-33	Sides of tank below water painted flat white
3	May 18-19	34-38	Lamp changed to a 300-W spot lamp shining through a 5-cm diameter hole (1° visual angle at center of tank, similar to that of sun)
4	May 19-June 4	39-58	Fluorescent room lights (out of direct view by smolts) left on
5	June 9-11	62-66	Shield on lamp removed; smolts placed in drum tank
6	June 15-30	67-82	No sheet over smolt during test

I asked the same questions as in 1971 but lack of sufficient data and a consistent, suitable test procedure made their solution difficult. Mean directions varied between the trilateral and pointing methods an average of 40.8°, 17.0° for tests with significant preferences. Strength of mean vectors were consistently much higher in the pointing method: $\bar{a}$ averaged 0.20 higher when pointings were recorded (0.12 for significantly strong preferences). Subsequent discussion will be for the trilateral results only.

A. QUESTION 1: DO SUBJECTS ORIENT?

1. Individuals

Calculating the mean interval size and $\bar{a}$ for each test treatment shows that these values changed after subjects were put in a smaller tank and the sheet removed (treatments 5 and 6):

Treatment number (Table 11, p. 79)	1	2	3	4	5	6
Mean independent interval (sec)	15.0	17.7	16.5	15.9	13.8	13.5
Mean $\bar{a}$	.16	.15	.22	.16	.29	.39

$\bar{a}$ values were transformed to arcsine $\sqrt{\bar{a}}$ (p. 35). The mean for treatments 1 to 4 was 0.14 and for 5 and 6 was 0.35; a highly significant increase (t-test, $p < .001$). Mean independence intervals in large and small tanks were 16.4 and 13.7, respectively; a significant reduction (t-test, $P < .01$). Thus, variation between successive pointings increased after treatment 5 but their distribution had a stronger central tendency.

Large tank results were analysed to see if stream origin or test time affected $\bar{a}$ and independence intervals. The same analysis would not be meaningful for the few small tank results. Means for each origin/time category are shown in Table 12. Each variable had to be analysed separately, i.e., interactions between origin and test time are assumed to be insignificant.

$\bar{a}$ values

Origin effects could be analysed with one-way analysis of variance. Results show that strength of individual orientations did not differ significantly between the four stocks ($F = 1.04$).

I used the Kruskal-Wallis non-parametric test to examine time effects because the variance of 16:00 results was unusually small. Again, no effect on $\bar{a}$ could be shown ($H = 0.10$).

Table 12. Mean $\overline{a}$ values and independence intervals for 1970 large tank tests. Upper figures: $\overline{a}$ values corresponding to means of arcsine $\sqrt{\overline{a}}$ transformed data. The number of tests are in brackets. Lower figures: mean independence intervals.

	Time			
Origin	12:00	16:00	Dusk	Mean
Fulton	0.18(5) 15.6	0.10(5) 15.0	0.09(3) 19.0	0.13(13) 16.2
Upper Babine	0.21(4) 17.3	0.21(4) 15.0	0.16(4) 19.5	0.19(12) 17.3
Lower Babine	0.07(4) 15.8	0.11(5) 14.4	0.17(5) 17.4	0.11(14) 15.9
Morrison	0.15(3) 17.0	0.12(4) 15.0	0.19(4) 18.0	0.15(11) 16.6
Mean	0.15(16) 16.3	0.12(18) 14.8	0.16(16) 18.4	0.14(50) 16.4

Independence intervals

The same non-parametric analysis was used for independence intervals. Intervals were not significantly different between origin groups (H = 5.03) but were different between test times (H = 11.34**). Table 12 (p. 81, column means) shows that variation between pointings was greatest at 16:00 and least at dusk.

Greater variability between successive pointings at 16:00 was related to increased swimming activity at this time. I found this by cumulating distances between successive head positions for each test. Every stock except Upper Babine was most active at 16:00. Upper Babine's activity changed little throughout the day.

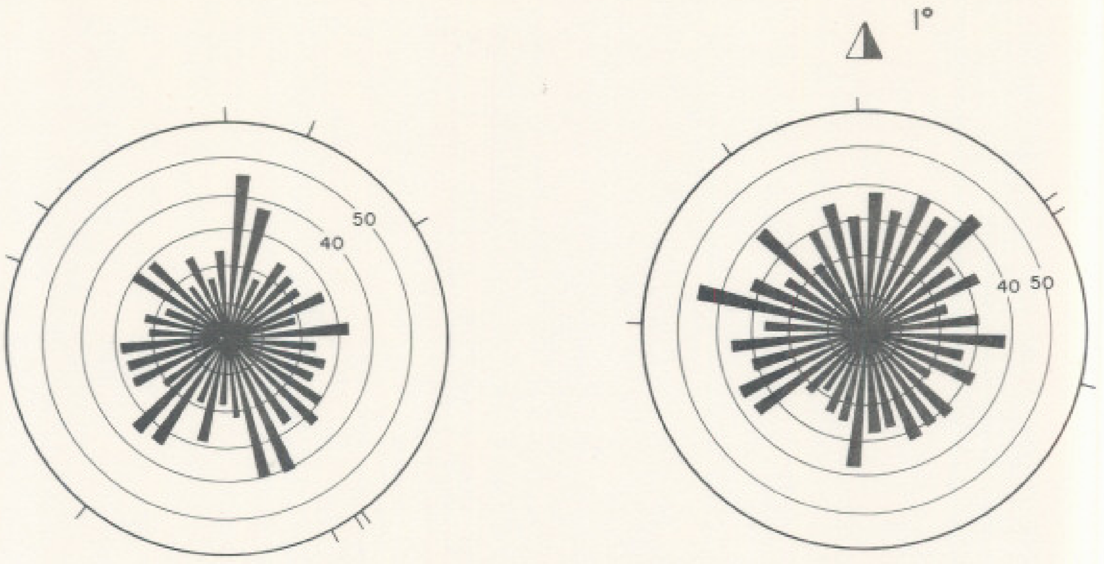
2. Samples

Only 35% of the smolts had significantly strong orientations but Fig. 15 and Table 13 show that most origin groups had significant, albeit weak, directional tendencies. Z statistics in Table 13 are for the distributions of significantly strong test mean directions and for the distributions of all independent directions. They show that Morrison and Lower Babine had the strongest group orientation. Fulton smolts preferred two directions and Upper Babine fish responded randomly (Fig. 15).

Differences between these samples are possibly not due to test time or tank size effects because all except Morrison have about equal numbers of tests at each time and in each tank:

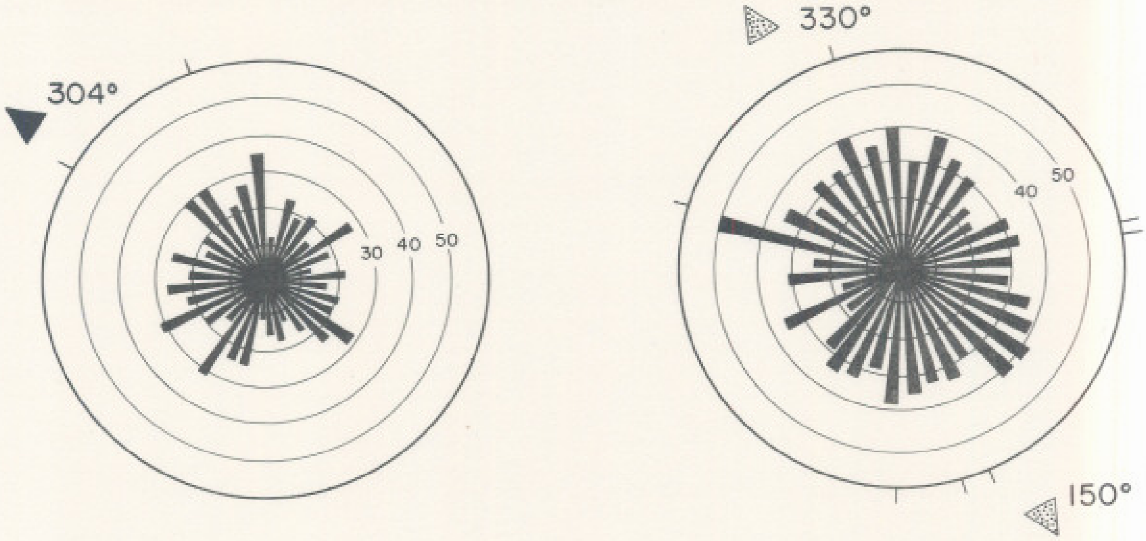
	Number of tests				
	Time			Tank	
	12:00	16:00	Dusk	Large	Small
Lower Babine	7	5	7	14	5
Upper Babine	5	7	6	12	6
Morrison	4	4	5	11	2
Fulton	8	5	5	13	5

Smolts, particularly Fulton smolts, were much more consistent in their directional preferences in small tanks (Table 14). Note that Z values for small tank tests are higher in almost every case. The median Z value for all small tank tests is 9.03** compared to 2.01 when I used large tanks. This makes the lower variation in the Morrison sample more impressive because they were only tested twice in small tanks:



UPPER BABINE

LOWER BABINE



MORRISON

FULTON

Fig. 15. Distribution of independent directions (central histogram) and test mean directions (on perimeter) for 1970 groups. See Fig. 10 (p. 41) for explanation of plots. Only significantly strong test means are shown.

Table 13. Summary of orientation by 1970 groups. Statistics describe the distribution of significantly strong test means as well as the distribution of all independent directions.

Origin	Significantly strong test means			Pooled independent directions		
	N	Mean	Z[a]	N	Mean	Z
Lower Babine	6	21	1.39	1134	1	3.34*
Upper Babine	9	72	0.02	964	147	1.70
		156-336	0.66			
Morrison	2	320	1.77	769	304	5.45**
Fulton	7	134	0.46	1156	61	0.19
					150-330	4.79**

[a] The Raleigh test is used here only as a rough indicator of dispersion because N is less than the allowable limit (12).

Table 14. Strength of orientation (Z) of 1970 smolts grouped by origin, test time, and test tank size. Missing values are due to too few tests (less than two).

Origin	Tank size[a]	Time		
		12:00	16:00	Dusk
Lower Babine	L.T.	1.51	0.05(1.80)[b]	0.19(1.12)
	S.T.	5.29**		6.76**
Upper Babine	L.T.	2.24	5.19**	3.04*
	S.T.		11.30**	1.10(7.94**)
Morrison	L.T.	5.52**	1.77	2.81
	S.T.			
Fulton	L.T.	2.29(5.80**)	0.37(0.51)	0.56
	S.T.	13.21**(16.87**)		22.66**

[a] L.T. = large test tank; S.T. = small test tank.

[b] Bracketed figures are Z statistics after the bimodal transformation (shown only if they are larger than the original Z).

	Number of tests			
	Lower Babine	Upper Babine	Morrison	Fulton
Large tanks	14	12	11	13
Small tanks	5	6	2	5

The effect of test time was less obvious. Median Z values for 12:00, 16:00, and dusk tests were 2.27, 1.07, and 1.69. Few values in each time group make it difficult to say whether preferences at noon are significantly less variable. The Z statistic for afternoon tests may be unduly low because there were only three small tank tests at this time:

	Number of tests		
	12:00	16:00	Dusk
Large tanks	16	18	16
Small tanks	8	3	7

Variation in directions chosen by smolts, regardless of their origin, was certainly least during noon tests. I pooled all independent directions for each time and found that Z was 22.23** at noon, 4.66** at 16:00, and 1.38 at dusk. This indicates that smolts of all origins preferred a similar direction at noon (334°) and, to a lesser extent, at 16:00 (160°).

B. QUESTION 2: DIFFERENCES IN PREFERRED DIRECTIONS

Directions from all four stocks were combined and four new samples repeatedly drawn at random to see if the observed differences in preferences could be expected by chance (p. 32). The stocks were significantly different since only 12 of 400 trials had greater B statistics ($P = .03$).

Since comparing all possible combinations is not a legitimate a priori technique, a type of a posteriori randomization test was designed which draws two groups out of the pooled data of all four groups. Their size is the only relation these groups have to the two actual samples. This is a much more conservative technique, therefore.

Both tests, the first pooling the two samples concerned and the second pooling all groups, led to identical conclusions (Table 15). Upper Babine smolts, which had no significant directional preference, differed from Lower Babine fish at a significance level of at least 5%. The Upper Babine response also differed significantly from Morrison's ($P < .01$). All other

Table 15. Comparisons of directional preferences for 1970 tests. Each cell contains the percent of B statistics for pairs of random groups (see p. 32) which exceed B for the two samples. Pairs of groups were drawn at random 200 times from the pooled data of the two samples (upper figure) and from the pooled data of all four samples (lower figure).

	Lower Babine	Upper Babine	Morrison	Fulton
Lower Babine		2.5* 0.5**	43.5 10.0	56.0 46.5
Upper Babine			0.0** 1.0**	38.5 44.5
Morrison				32.0 8.5
Fulton				

combinations were not significantly different. I confirmed that Morrison, Lower Babine, and Fulton were homogenous with respect to directional preferences by using the randomization test with Upper Babine omitted from the data pool (P = .175, 200 trials).

C. QUESTION 3: ADAPTIVENESS OF DIRECTIONAL PREFERENCES

Table 13 (p. 85) shows that, for pooled independent directions, Lower Babine had a significant preference for North (1°). This was not significantly different from the expected direction of 350° (Stephen's test, $P \gg .05$). Upper Babine smolts did not have any significant preference. The Fulton sample may have adaptive bimodal orientation because one mode (330°) is very similar to the expected direction (335°).

Morrison's preference of 304° falls within the expected seasonal shift in migration directions. I looked at the seasonal changes in weekly mean directions for each group as in 1971 but no trends could be detected.

D. ORIENTATION MECHANISMS

I examined constant angle orientation, C.A.O., as before (p. 55) by comparing dispersions before and after making the lamp azimuth equal to 0°. Comparison of Z values between the columns in Table 16 shows that Upper Babine and Fulton samples were better oriented after this transformation. This indicates that C.A.O. was predominant in these groups, Upper Babine preferring a direction 141° to the left of the lamp and Fulton pointing away from it (Table 16). The former's preference of 141° is significantly different from 180° (Stephen's test, $.01 < P < .05$) so it is not purely negative phototaxis as suggested by Fulton's response. Lower Babine and especially Morrison smolts oriented more precisely relative to North.

The effect of tank size on the C.A.O. of Upper Babine and Fulton stocks is shown in Table 17 where the same analysis as above was repeated. The transformation increased Z values most in small tank tests. It appears that C.A.O. was enhanced in smaller tanks.

Negative orientations to the light source were very striking in the noon tests (Table 18). This explains why preferences were more precise at noon (p. 87). All four groups pointed away from the light, means falling between 150-168°. Furthermore, all four means were significantly strong but only two significant preferences occurred later in the day even though lamp azimuth and altitude remained unchanged. Perhaps this reflects a change in motivation controlled by circadian rhythm mechanisms.

Table 16. Summary of orientation relative to lamp direction by 1970 groups.

	Lamp azimuth = Sun azimuth			Lamp azimuth = 0°		
	Mean	$\bar{a}$	Z	Mean	$\bar{a}$	Z
Lower Babine	1	.05	3.34*	140	.04	2.26
Upper Babine	147	.04	1.70	219	.08	6.93**
Morrison	304	.08	5.45**	190	.00	0.00
				104-284	.01	0.08
Fulton	61	.01	0.19	176	.09	9.87**
	150-330	.06	4.79**			

Table 17. Effect of test tank on orientation to the light source by 1970 Upper Babine and Fulton stocks.

	Lamp azimuth = Sun azimuth		Lamp azimuth = 0°	
	Mean	Z	Mean	Z
Upper Babine				
Large tanks	156	2.10	242	4.61**
Small tanks	93	0.17	186	4.42**
	179-359	1.74	80-260	6.10**
Fulton				
Large tanks	262	0.70	79	0.87
	109-289	1.25	117-297	3.16*
Small tanks	74	3.74*	190	33.70**
	162-342	15.21**		

Table 18. Directional preferences of 1970 groups at each test time. Figures in brackets are the directions relative to the lamp direction (lamp = 0°).

	Noon	Afternoon	Dusk
Mean sun azimuth	172	252	302
Upper Babine	326** (150**)[a]	142** (251**)	163 (230)
Lower Babine	340* (168*)[a]	10-190 (121-301)	40 (91)
Morrison	335** (162**)[a]	219 (328)	294 (352)
Fulton	334** (164**)[a]	179 (288)	132** (178**)[a]

[a] Not significantly different from 180° (P = .05).

APPENDIX B

TEMPORAL ASSOCIATION OF POINTINGS AND ACTIVITY IN 1971

A. TEMPORAL ASSOCIATION OF POINTINGS

Intervals of independence are valuable as a behavioral description as well as providing a proper statistical base for vector analysis of orientation. A smolt oriented in a similar direction for several successive pointings will result in a large interval and an active smolt usually decreases the interval size. Clusters of pointings around the compass may have a weak mean vector ($\bar{a}$) although successive pointings may be close together. I analyzed the temporal association between pointings (T.A.) with respect to stream origin, test time (date and time of day), and test treatment.

I regressed independence intervals on date (days since April 1) to see if there was a seasonal effect on T.A. This was done with each origin/time/test location category for Major and Holding groups. Of the nine indoor and 12 outdoor cells only three had significant trends. I conclude that time of season was not a significant factor.

Appendix C (p. 103) shows the mean interval size for each origin/time/test location category (bottom figures). Comparing these means between times of day reveals no pattern so I conclude that T.A. was also not significantly different between times of day.

Consequently, I pooled the data from all test times and calculated a grand mean for indoor and outdoor tests of each stock (Table 19). Larger independence intervals for outdoor tests showed that smolts generally had greater T.A. between pointings in these tests. Mean "independence curves" show this in more detail (Fig. 16).

Looking now at the effect of their stream origin, I compared the means within each column of Table 19 excluding the Holding group. Of the 10 indoor and 10 outdoor comparisons, only four differences were significant, all in outdoor tests:

1. Upper Babine - Fulton; t = 2.94**
2. Upper Babine - Morrison; t = 2.46*
3. Upper Babine - Pinkut; t = 2.73**
4. Lower Babine - Pinkut; t = 2.19*

Upper Babine had an unusually great tendency to cluster pointings. The pattern of interval sizes is not consistent between indoor and outdoor series. I conclude that origin also had an insignificant effect on T.A.

The difference in interval size between Holding smolts (7.1) and their parent Morrison group (7.8) was not significant either. It appears, therefore, that the type of test, indoor or outdoor, was the only factor examined which affected the association or independence of successive pointings.

Table 19. Mean independence intervals for indoor and outdoor tests of 1971 Main Stocks.

Origin	Indoor tests	Outdoor tests	t statistic[a]
Fulton	6.8	7.4	1.43
Upper Babine	6.8	8.4	2.60*
Morrison	6.7	7.8	3.24**[b]
Lower Babine	7.5	7.5	0.00
Pinkut	6.0	6.8	1.27
Morrison (Holding)		7.1	

[a] Test of null hypothesis that independence intervals are the same for indoor and outdoor tests.

[b] Determined by Approximate t-test (Sokal and Rohlf 1969) because variances of outdoor and indoor groups were significantly different.

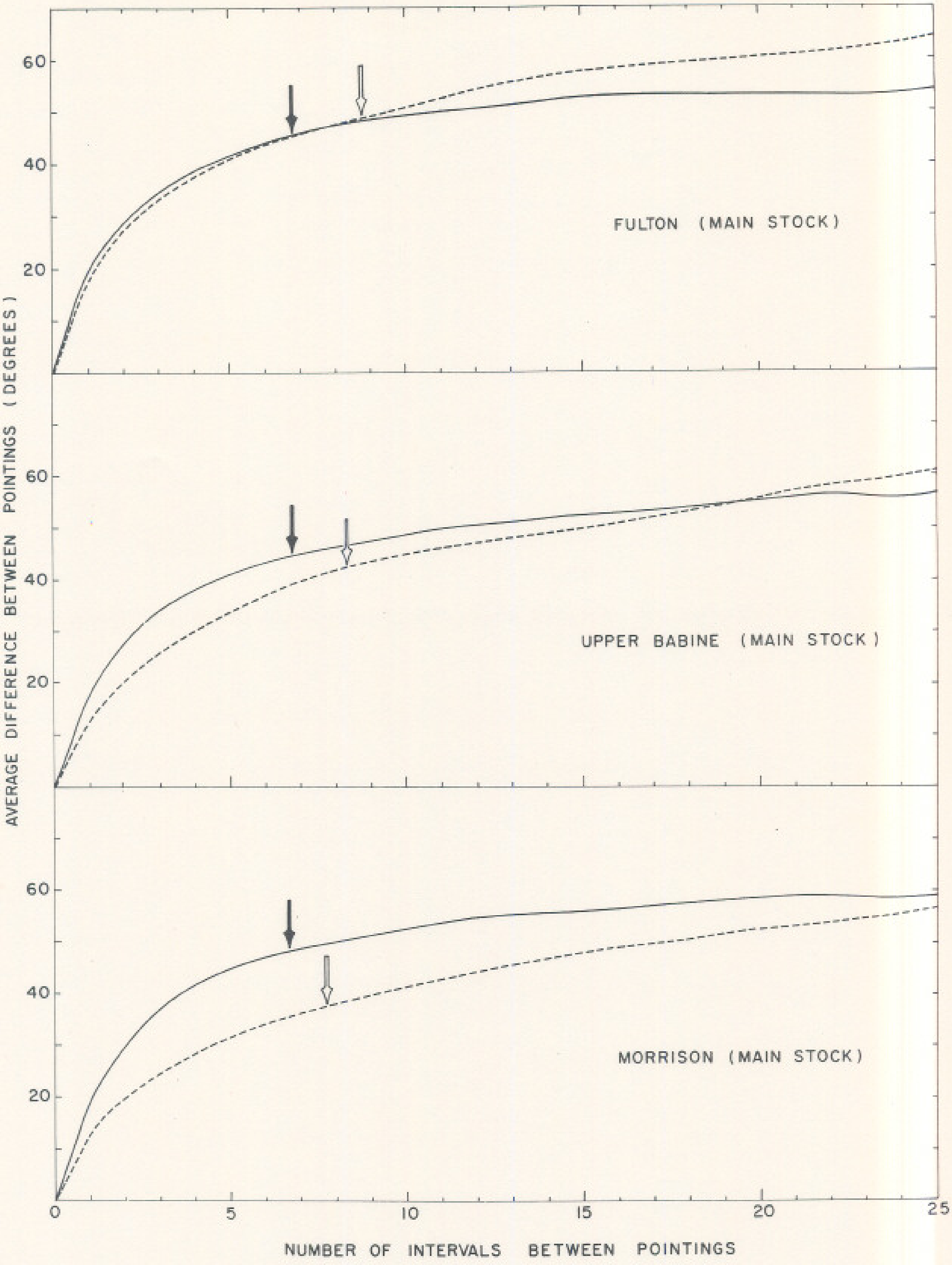


Fig. 16. Mean independence curves for indoor (solid line) and outdoor (broken line) tests of Major Groups. Arrows indicate points of independence.

B. ACTIVITY

Activity was inferred from N, the total number of pointings in each test before the independence calculation: more active smolts make fewer pointings. Table 11 shows the mean N for each origin/test location group (columns 4 and 8 from the left). Indoor smolts were obviously more active. These mean activity estimates are positively correlated with corresponding independence intervals (Table 19, p. 96). The correlation was significant at the 5% level outdoors and 1% level indoors (Kendall rank correlation). The correlation using individual interval sizes and n's for all 331 Main Stock tests, excluding Holding, was highly significant (t = 212.9***, Kendall rank correlation). Thus, temporal association between pointings was greater in less active smolts.

I analyzed the effects of test location, time of day, and origin on activity of Main Stocks (excluding Holding) using unbalanced 3-way analysis of variance (Bram 1970). Table 21 shows that all first and second order interactions between these factors were insignificant. Consequently, I was free to examine main effects.

The test location effect was highly significant ($P < .001$). This confirms that smolts tested indoors, which probably clustered successive pointings less because independence intervals are smaller, were markedly more active than outdoors.

Analysis of variance also reveals a significant difference between times of day ($P < .05$) which Table 20 shows is an increase in activity or decrease in N at dusk. Note that smolts were more active at dusk in both test series.

Activity was not significantly different between Main Stocks (Table 21).

Changes in activity during the season cannot be analyzed because pointings were recorded more selectively as the season progressed (p. 29).

Table 20. Mean number of pointings in 1971 Main Stock tests.

Origin	Indoor tests				Outdoor tests				Grand mean
	12:00	16:00	Dusk	Mean	12:00	16:00	Dusk	Mean	
Fulton	126.7	126.3	81.5	111.1	170.1	148.2	137.2	152.2	139.2
Upper Babine	141.8	141.6	123.9	135.2	156.9	154.9	128.8	147.2	143.6
Morrison	135.6	141.4	94.6	123.3	148.4	176.8	166.8	164.6	151.3
Lower Babine	188.0	111.5	194.5	164.7	234.8	206.0	134.0	203.1	192.1
Pinkut	100.5	82.0	69.0	83.8	171.3	136.7	152.4	153.5	135.3
Morrison (Holding)					186.0	155.7	98.4	141.0	
Mean	125.5	123.2	110.3	119.5	165.6	154.7	138.0	152.7	143.9

Table 21. Three-way analysis of variance to test differences in activity between time and location categories of the three Major Groups. The total number of pointings, N, in a test was used as an estimate of activity.

Source of variation	df	SS	MS	F
Between locations	1	66,096[a]	66,096	12.46***
Between origin groups	2	7,581[a]	3,791	0.71
Between times	2	38,576[a]	19,288	3.63*
Location × origin	2	12,812	6,406	1.21
Location × time	2	5,737	2,869	0.54
Time × origin	4	14,071	3,518	0.66
Location × time × origin	4	10,995	2,749	0.52
Error	313	1,660,900	5,307	
Total	330	1,817,160		

[a] Main effects SS calculated using the fact that first or second order interactions are insignificant (Bram 1970).

APPENDIX C

SUMMARIES OF 1970-71 TEST DATA

1970 INDOOR TESTS

Date	1200					1600					Dusk				
	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]
								FULTON							
Apr. 16	15	68	182	.22	*	15	70	118	.14		15	75	317	.11	
30	18	51	130	.10		15	59	284	.07		21	55	63	.03	
May 7	18	52	75	.09		15	65	47	.06		21	50	65	.15	
21	15	54	323	.11		15	56	201	.11						
June 4	12	68	287	.46	**	15	54	231	.12						
11	12	73	158	.37	**										
18	12	64	77	.23	*						12	78	165	.65	**
30	9	95	342	.86	**						12	69	80	.34	**
$\bar{x}$	14	66		.31		15	61		.10		16	65		.26	
								UPPER BABINE							
Apr. 14	15	57	135	.11		15	58	143	.33	**					
28	15	62	21	.23	*	15	56	118	.10		12	67	337	.02	
May 5	15	57	48	.11		15	64	220	.23	*	27	34	152	.62	**
19	24	33	306	.42	**	15	55	239	.20		18	46	352	.05	
June 2											21	50	138	.14	
9						15	58	359	.24	*	15	63	347	.18	
16						18	42	58	.41	**	18	40	228	.23	
25	18	56	291	.46	**	15	66	145	.69	**					
$\bar{x}$	17	53		.27		15	57		.31		19	50		.21	
								LOWER BABINE							
Apr. 15						15	57	96	.11		15	61	256	.10	
29	18	45	1	.05		15	57	314	.09		15	60	105	.32	**
May 6	18	50	219	.01		15	64	269	.15		21	43	119	.15	
20	12	67	267	.13		12	63	77	.15		15	63	274	.15	
June 3	15	66	297	.15		15	59	248	.05		21	43	287	.18	
10	12	78	273	.23	*						15	60	59	.45	**
17	12	65	55	.41	**										
29	15	63	359	.27	*						12	70	324	.22	*
$\bar{x}$	15	62		.18		14	60		.11		16	57		.22	

1970 INDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]	Independence Time[a]	Sample Size	Mean Direction	$\bar{a}$	p[b]
								MORRISON							
Apr. 13						15	55	261	.13						
27											15	68	154	.07	
May 4	27	31	360	.14		12	64	159	.13		27	31	300	.48	**
18	12	79	340	.37	**	15	55	208	.10		15	58	309	.19	
June 1	12	72	160	.02		18	47	252	.13		15	56	228	.11	
22	12	73	320	.19							12	80	16	.06	
$\bar{x}$	16	64		.18		15	55		.12		17	59		.18	

[a] Time is equal to number of intervals times 3 seconds.

[b] P is the probability that the distribution is random.

1971 INDOOR TESTS

Date	1200					1600					Dusk				
	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	p^a
						FULTON (main stock)									
Apr. 15	11	21	358	.35	.06	9	21	163	.51	.00	6	26	67	.44	.00
19	7	30	353	.50	.00	8	28	195	.34	.02	6	20	284	.84	.00
26	9	19	273	.44	.01	9	20	241	.46	.00	6	17	287	.56	.00
May 3	6	24	177	.63	.00	11	10	39	.37	.25	7	29	42	.76	.00
10	7	5	299	.99	.00	6	10	284	.94	.00	8	6	182	.10	.93
17	6	14	166	.73	.00	6	13	266	.80	.00	5	14	291	.99	.00
25	6	20	347	.41	.02	8	12	324	.84	.00	11	2	28	.70	.37
31	4	27	221	.72	.00	7	23	347	.29	.12	5	12	102	.98	.00
June 7	9	24	98	.87	.00	8	6	200	.36	.45	6	12	332	.75	.00
14	5	11	138	.79	.00	5	14	277	.69	.00	4	7	289	.98	.00
21	5	4	173	.99	.01	6	39	56	.37	.00	4	8	278	.92	.00
28	-	0	-	-	-	6	11	48	.72	.00	5	13	286	.99	.00
$\bar{x}$	6.8	16.6		.67		7.4	17.3		.56		6.1	13.8		.75	
						UPPER BABINE (main stock)									
Apr. 13											7	21	335	.24	.29
20	7	27	187	.16	.50	9	26	60	.65	.00	7	25	179	.63	.00
27	9	29	46	.73	.00	8	25	198	.51	.00	12	19	279	.39	.03
May 4	8	24	174	.87	.00	7	31	139	.17	.41	6	21	248	.32	.10
11	7	33	321	.88	.00	4	19	8	.87	.00	5	28	256	.97	.00
18	4	17	176	.74	.00	5	21	228	.68	.00	5	10	289	.72	.00
26	5	13	210	.59	.00	5	8	44	.80	.00	5	12	87	.96	.00
June 1	9	23	62	.89	.00	8	36	287	.77	.00	7	20	334	.78	.00
8	9	19	317	.42	.01	6	16	256	.95	.00	10	10	109	.86	.00
15	5	11	76	.26	.47	5	11	203	.92	.00	8	13	56	.76	.00
22	7	7	222	.45	.23	5	21	247	.97	.00	7	16	80	.77	.00
29	9	8	120	.55	.07	-	0	-	-	-	5	21	113	.86	.00
$\bar{x}$	7.2	19.2		.59		6.2	19.4		.73		7.0	18.0		.69	
						MORRISON (main stock)									
Apr. 14	5	38	14	.22	.16	5	51	267	.97	.00	7	18	265	.56	.00
21	5	45	133	.81	.00	7	30	198	.56	.00	7	19	169	.50	.00
28	9	26	289	.59	.00	10	25	14	.64	.00	6	40	182	.92	.00
May 5	6	38	162	.93	.00	6	24	342	.70	.00	8	16	276	.66	.00

1971 INDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a
MORRISON (main stock)															
May 12	8	8	186	.75	.00	7	12	337	.73	.00	5	18	14	.88	.00
19	6	20	300	.48	.00	6	14	346	.94	.00	7	8	218	.84	.00
27	7	9	314	.48	.10	8	16	27	.80	.00	8	4	289	.84	.03
June 2	5	22	318	.46	.00	6	22	347	.25	.24	4	5	170	.30	.64
9	6	19	76	.71	.00	7	16	333	.46	.02	10	1	191		
16	6	12	176	.98	.00	7	12	176	.78	.00	6	6	99	.78	.01
23	5	9	112	.97	.00						8	1	350		
30	6	27	351	.49	.00	6	12	107	.59	.00	8	32	95	.77	.00
$\bar{x}$	6.2	22.8		.66		6.8	21.3		.67		7.0	14.0		.71	
LOWER BABINE (main stock)															
June 6	8	21	151	.30	.13	5	11	38	.92	.00	10	20	288	.39	.03
26	8	26	43	.19	.38	7	24	251	.70	.00	7	27	156	.71	.00
$\bar{x}$	8.0	23.5		.25		6.0	17.5		.81		8.5	23.5		.55	
PINKUT (main stock)															
June 5	4	10	158	.99	.00	7	14	324	.31	.26	6	8	184	.22	.67
27	7	23	151	.93	.00	6	11	150	.78	.00	6	15	80	.95	.00
$\bar{x}$	5.5	16.5		.96		6.5	12.5		.55		6.0	11.5		.59	
FULTON EGG STOCK (small tanks)															
May 29	12	4	32	.41	.51	5	10	117	.42	.15	4	49	142	.99	.00
30	5	15	286	.91	.00	8	10	245	.45	.11	5	37	115	.98	.00
$\bar{x}$	8.5	9.5		.66		6.5	10.0		.44		4.5	43.0		.99	
FULTON (small tanks)															
June 12	6	17	189	.84	.00	7	18	344	.40	.03	4	33	308	.99	.00
13	4	17	237	.84	.00	6	6	71	.88	.00	5	24	176	.39	.01
$\bar{x}$	5.0	17.0		.84		6.5	12.0		.64		4.5	28.5		.69	

1971 INDOOR TESTS (cont'd)

Date	1200					1600					Dusk				
	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p[a]	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p[a]	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p[a]
MORRISON (small tanks)															
June 19	5	11	325	.79	.00	6	4	130	.53	.32	5	10	107	.38	.23
20	6	3	245	.44	.56	6	18	1	.60	.00	6	44	116	.94	.00
$\bar{x}$	5.5	7.0		.62		6.0	11.0		.57		5.5	27.0		.66	

[a] P is the probability that the distribution is random.

1971 OUTDOOR TESTS

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a
FULTON (main stock)															
Apr. 15	5	39	269	.93	.00	6	40	288	.86	.00					
19	5	35	30	.95	.00	8	25	323	.20	.37	6	26	172	.21	.33
26	4	32	21	.38	.00	6	15	109	.30	.26	5	40	345	.97	.00
May 3	5	40	271	.87	.00	6	41	178	.97	.00	7	31	22	.22	.20
10	6	20	91	.94	.00	7	26	209	.90	.00					
	7	19	133	.60	.00	5	23	226	.66	.00					
	6	21	199	.36	.05	8	17	109	.63	.00	6	7	137	.39	.33
17	10	25	108	.22	.29	7	36	72	.59	.00	-	0	-	-	-
	12	19	178	.60	.00	10	28	39	.81	.00	9	22	42	.33	.08
	7	33	110	.17	.37	11	24	256	.81	.00	8	27	299	.24	.19
25	11	15	183	.75	.00	5	12	129	.70	.00	7	14	165	.64	.00
	6	29	185	.71	.00	5	28	205	.41	.00	7	27	295	.65	.00
	8	22	18	.47	.00	8	23	18	.62	.00	8	30	248	.62	.00
31	12	18	295	.85	.00	9	2	279	.99	.12	5	9	322	.61	.02
											5	10	308	.41	.18
	7	23	310	.82	.00	7	2	36	.99	.11	11	16	309	.49	.00
June 7	6	7	352	.99	.00	8	15	203	.44	.03	5	18	252	.61	.00
	7	19	205	.33	.11	6	14	91	.88	.00	9	3	191	.44	.56
	6	14	60	.27	.35	7	20	308	.30	.15	6	20	299	.30	.15
14	7	34	110	.92	.00	9	22	330	.44	.00	7	13	327	.58	.00
	12	19	242	.51	.00	9	19	321	.76	.00	7	25	76	.29	.11
											8	17	171	.43	.02
21	7	32	133	.72	.00	7	4	45	.76	.08	7	21	50	.19	.47
	6	26	122	.48	.00	5	15	232	.53	.00	6	6	80	.61	.09
	9	18	260	.34	.11	7	21	98	.12	.75	5	9	250	.32	.39
28	11	21	24	.26	.24	11	16	79	.26	.33	8	32	132	.83	.00
	4	56	56	.67	.00	12	16	29	.48	.01	10	18	292	.41	.03
	11	2	94	.89	.19	10	10	184	.44	.12	6	27	94	.49	.00
$\bar{x}$	7.6	24.5		.62		7.7	19.8		.61		7.0	18.7		.47	
UPPER BABINE (main stock)															
Apr. 20	12	17	14	.45	.01	8	26	34	.58	.00	5	14	275	.62	.00
27	7	26	58	.63	.00	8	26	284	.37	.01	6	27	105	.24	.19
May 4	9	19	216	.26	.26	6	24	301	.13	.66	9	22	99	.71	.00
11	7	17	81	.62	.00	10	6	261	.52	.19	6	4	255	.50	.36
	9	22	248	.75	.00	10	21	120	.77	.00	12	18	130	.32	.15
	9	18	20	.63	.00	7	10	271	.29	.42	7	9	82	.32	.38

1971 OUTDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a
								UPPER BABINE (main stock)							
May 18	10	20	189	.82	.00	8	11	350	.18	.68	11	16	342	.43	.03
	7	15	4	.24	.40	8	10	140	.80	.00	9	2	80	.72	.35
	12	23	33	.15	.60	9	18	209	.15	.66	10	11	193	.78	.00
26	10	18	174	.47	.00	12	17	22	.33	.14	-	0	-	-	-
	5	21	185	.61	.00	9	25	226	.73	.00	12	16	233	.75	.00
	8	26	151	.87	.00	9	20	184	.75	.00	10	18	171	.61	.00
June 1	5	7	8	.99	.00	7	24	104	.82	.00	6	34	142	.34	.00
	7	23	83	.63	.00	9	28	138	.64	.00	8	12	74	.79	.00
	11	6	44	.67	.04	7	25	252	.26	.17	7	30	293	.29	.06
8	5	43	303	.96	.00	10	12	9	.16	.73	9	11	123	.32	.32
	5	36	353	.33	.00	6	46	310	.78	.00	6	18	49	.70	.00
	10	20	88	.16	.61	9	14	208	.06	.94	12	19	303	.63	.00
15	8	9	333	.59	.02	8	28	167	.54	.00	8	21	310	.93	.00
	6	11	317	.29	.40	10	21	256	.77	.00	5	26	343	.47	.00
	6	10	124	.44	.13	9	2	276	1.0	.11	9	3	158	.85	.09
22	5	11	258	.87	.00	11	18	67	.47	.01	5	6	62	1.0	.00
	10	9	151	.49	.09	6	9	257	.71	.00	10	19	159	.22	.38
						7	6	267	.58	.11	6	1	339	-	-
29	8	36	26	.56	.00	8	10	356	.24	.55	8	23	190	.54	.00
	13	21	187	.30	.14	8	21	15	.61	.00	-	0	-	-	-
	13	16	209	.48	.01	8	29	263	.10	.75	12	11	62	.77	.00
$\bar{x}$	8.3	19.2		.55		8.4	18.8		.49		8.3	14.5		.58	
								MORRISON (main stock)							
Apr. 14											7	18	15	.55	.00
21	4	39	96	.68	.00	8	30	200	.93	.00	4	54	180	.61	.00
28	8	26	184	.81	.00	4	48	265	.97	.00	6	36	342	.27	.06
May 5	5	9	110	.20	.68	6	39	302	.16	.39	12	20	341	.15	.62
12	7	12	322	.79	.00	8	12	65	.78	.00	5	1	213	-	-
	12	11	278	.56	.01	6	12	134	.19	.65	9	18	201	.36	.08
	8	11	173	.98	.00	-	0	-	-	-	12	17	329	.38	.07
19	6	25	137	.56	.00	8	23	304	.44	.00	8	14	187	.34	.18
	4	40	155	.90	.00	10	24	147	.74	.00	11	18	279	.72	.00
	8	31	206	.66	.00	7	29	189	.48	.00	12	11	30	.17	.73
27	10	11	255	.55	.02	9	24	351	.69	.00	6	5	18	.36	.52
	9	25	249	.83	.00	11	22	306	.29	.13	6	9	44	.56	.04

1971 OUTDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{a}$	p^a
MORRISON (main stock)															
May 27	6	41	103	.90	.00	8	19	164	.53	.00	8	6	209	.28	.62
June 2						5	20	340	.48	.00	8	20	206	.50	.00
						8	31	249	.45	.00	6	49	82	.92	.00
						6	42	160	.92	.00	7	39	328	.78	.00
9	8	26	347	.85	.00	6	13	340	.45	.05	11	22	49	.83	.00
	9	19	15	.70	.00	8	8	0	.76	.00	11	21	168	.33	.08
	8	25	214	.78	.00	6	12	144	.44	.07	8	15	117	.14	.75
16	8	9	333	.59	.02	8	28	167	.54	.00	8	21	310	.93	.00
	6	11	317	.29	.40	10	21	256	.77	.00	5	26	343	.47	.00
	6	10	124	.44	.13	9	2	276	1.0	.11	9	3	158	.85	.09
23	4	2	198	.46	.65	8	27	278	.64	.00	6	7	324	.42	.29
	9	27	299	.77	.00	9	28	287	.87	.00	10	27	267	.44	.00
											11	24	78	.58	.00
30						10	24	22	.28	.13	8	36	295	.67	.00
	6	24	305	.25	.20	9	16	305	.36	.11	-	0	-	-	-
	8	30	298	.71	.00	10	23	125	.28	.15	7	12	95	.70	.00
$\bar{x}$	7.2	21.1		.65		7.9	22.2		.58		8.2	19.6		.51	
LOWER BABINE (main stock)															
June 6	10	20	288	.39	.03	6	51	334	.99	.00					
	8	19	78	.13	.71	8	19	352	.87	.00					
	7	39	242	.99	.00	10	27	80	.79	.00					
26	8	38	325	.68	.00	9	27	355	.73	.00	6	36	287	.75	.00
	10	24	232	.82	.00	7	31	141	.72	.00	6	15	167	.70	.00
	5	48	108	.34	.00	6	8	214	.83	.00	6	16	184	.21	.48
$\bar{x}$	8.0	31.3		.56		7.7	27.2		.82		6.0	22.3		.55	
PINKUT (main stock)															
June 5	7	12	359	.64	.00	6	24	306	.22	.30	8	26	199	.01	.99
	11	22	102	.43	.00	5	7	43	.48	.19	8	29	145	.83	.00
	8	21	167	.66	.00	5	7	344	.09	.94	5	3	181	.93	.05
27	6	29	106	.90	.00	6	37	137	.57	.00	4	5	70	.59	.16
	9	21	81	.77	.00	6	40	235	.73	.00	7	41	335	.79	.00

1971 OUTDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{r}^a$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{r}^a$	p^a	Independent Interval	Sample Size	Mean Direction	$\bar{r}^a$	p^a
PINKUT (main stock)															
June 27	9	19	95	.72	.00	6	24	225	.16	.54					
$\bar{x}$	8.3	20.7		.69		5.7	23.2		.38		6.4	20.8		.63	
MORRISON/HOLDING (main stock)															
Apr. 22						6	14	1	.10	.87					
29	9	14	326	.34	.18	7	35	207	.56	.00	7	32	213	.56	.00
May 6	6	39	111	.91	.00	8	12	15	.64	.00	5	23	231	.64	.00
13	10	19	289	.54	.00	8	28	14	.65	.00	6	22	45	.85	.00
	10	22	105	.29	.13	5	48	20	.63	.00	3	82	66	.94	.00
	10	17	284	.28	.24	7	20	305	.94	.00	8	30	316	.13	.61
20	9	22	62	.84	.00	6	20	37	.47	.00	10	27	153	.95	.00
	7	21	92	.87	.00	8	27	217	.83	.00	8	8	25	.96	.00
	8	25	85	.47	.00	10	20	355	.60	.00	6	9	96	.81	.00
28	6	35	82	.96	.00	6	4	264	.89	.02	3	73	266	.99	.00
	8	13	310	.49	.02	9	26	256	.55	.00	-	0	-	-	-
	8	26	80	.31	.06	8	27	299	.69	.00	4	7	201	.30	.53
June 3						6	24	69	.03	.97	-	0	-	-	-
						7	31	57	.86	.00	4	5	60	.32	.60
						5	12	191	.99	.00	5	6	152	.85	.00
10						8	13	203	.93	.00	8	15	48	.74	.00
						9	15	74	.60	.00	7	4	22	.57	.26
						10	19	322	.73	.00	6	15	266	.38	.10
17	11	19	191	.31	.14	11	14	167	.60	.00	5	2	46	.10	.97
						5	19	320	.45	.01	4	9	241	.45	.15
											8	2	116	.96	.14
24	7	28	85	.85	.00	4	2	113	1.0	.12	5	4	337	.24	.79
						10	24	241	.86	.00	7	3	288	.98	.03
											7	1	328	-	-
July 1	6	32	318	.19	.33	9	23	28	.39	.01	11	23	67	.26	.19
						6	24	116	.67	.00	4	5	21	.78	.03
											-	0	-	-	-
$\bar{x}$	8.2	23.7		.55		7.4	20.9		.65		6.1	15.7		.63	
FULTON EGG STOCK (small raising tanks)															
May 29	6	9	344	.98	.00	12	21	113	.65	.00	9	21	318	.61	.00

1971 OUTDOOR TESTS (cont'd)

	1200					1600					Dusk				
Date	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	P[a]	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	P[a]	Independent Interval	Sample Size	Mean Direction	$\bar{r}$	P[a]
						FULTON EGG STOCK (small raising tanks)									
May 29	10	7	249	.89	.00	8	8	39	.89	.00	12	22	199	.83	.00
	6	10	317	.99	.00	9	27	250	.61	.00	10	24	43	.66	.00
30	12	20	310	.63	.00	12	14	48	.50	.01	8	14	223	.32	.23
	10	27	165	.25	.18	9	7	40	.78	.00	11	18	162	.26	.29
	10	19	19	.63	.00	8	31	185	.87	.00	6	8	119	.04	.98
$\bar{x}$	9.0	15.3		.73		9.7	18.0		.72		9.3	17.8		.45	
						FULTON (small raising tanks)									
June 12	7	13	282	.58	.00	5	9	4	.42	.19	7	28	165	.30	.07
	6	11	240	.83	.00	4	2	156	.96	.14	5	52	279	.97	.00
	5	48	97	.98	.00	7	15	157	.45	.03	-	0	-	-	-
13	11	24	6	.53	.00	6	35	45	.56	.00	10	19	234	.40	.03
	5	8	31	.48	.14	4	5	20	.25	.72	-	0	-	-	-
	4	33	337	.85	.00	7	2	152	.20	.92	6	6	253	.87	.00
$\bar{x}$	6.3	22.8		.71		5.5	11.3		.47		7.0	17.5		.64	
						MORRISON (small raising tanks)									
June 19	6	26	349	.75	.00	10	23	121	.46	.00	11	22	288	.31	.10
	7	11	66	.58	.01	6	12	156	.52	.02	7	27	188	.52	.00
	11	26	55	.61	.00	7	39	319	.89	.00	7	24	279	.23	.26
20	7	37	244	.23	.13	8	7	178	.58	.07	6	1	278	-	-
	9	17	71	.32	.15	7	6	291	.09	.95	6	14	353	.37	.13
	5	18	253	.40	.04	3	19	89	1.0	.00	-	0	-	-	-
$\bar{x}$	7.5	22.5		.48		6.8	17.7		.59		7.4	14.7		.36	

[a] P is the probability that the distribution is random.