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The Use of Celestial and Magnetic Cues by Orienting Sockeye Salmon Smolts

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Summary. 1. Yearling sockeye salmon (smolts), *Oncorhynchus nerka*, trapped at the outlet of Babine Lake, Canada, on their way from the lake downstream to the ocean were tested in round orientation tanks. With a view of the sky, the smolts oriented towards the lake's outlet in the normal magnetic field (Fig. 3) and in a field rotated 90° counterclockwise (Fig. 4).

2. Under opaque covers, the smolts displayed a bimodal distribution. In the normal magnetic field, they oriented towards or away from the lake's outlet (Fig. 5). In the altered field, the axis of the distribution was rotated 56° away from the axis in the normal field (Fig. 6).

Introduction

Unlike the other species of Pacific salmon which reside in rivers or migrate directly to the ocean after emergence from gravel nests, sockeye salmon (*Oncorhynchus nerka*) are obligate lake dwellers for the first year of their lives. The migration from stream incubation area to lake nursery area is controlled by complex rheotactic and olfactory responses (Brannon 1967, 1972; Raleigh 1967, 1971; Bodznick 1978a, b). The dispersal migration in the nursery lake is aided by compass directional preferences (Brannon 1972). These compass preferences have an innate, population-specific, component (Brannon et al. 1981) and are guided by celestial and magnetic cues (Quinn 1980, 1981; Quinn et al. 1981).

After a year, sockeye smolts migrate to the outlet of their nursery lake and travel downstream to the ocean. Johnson and Groot (1963) and Groot (1965) reported that smolts from Babine Lake, British Columbia, Canada, displayed preferences for the direction of the lake's outlet when tested in round arenas. This finding was supported by SONAR studies indicating that movement to the outlet was well directed, rapid, and generally occurred near dawn and dusk (Groot and Wiley 1965; Groot 1972). Subsequent arena tests suggested that populations within the lake have genetically distinct directional preferences (Simpson 1979).

Groot (1965) concluded that the smolts make use of the sun's position and light polarization patterns as guidance mechanisms. However, when he eliminated these cues, smolts generally oriented either towards or away from the lake's outlet. He concluded that there was a non-visual guidance mechanism operating in addition to the celestial mechanisms. Recent research has shown that sockeye fry can orient in the absence of visual cues, using the earth's magnetic field (Quinn 1980). The present study was designed to investigate the hypothesis that the magnetic field is the mechanism which complements the visual guidance systems in orienting smolt migrations across open water.

Materials and Methods

Study Site and Population. Babine Lake is roughly 150 km long, drained by Babine River into the Skeena River in northern British Columbia (Fig. 1). It presently supports a very large sockeye population (smolt outmigration was estimated at 108 million in 1979, 55 million in 1980, and 193 million in 1981; source: Department of Fisheries and Oceans, Canada). While adult sockeye spawn in many tributaries in the lake, Babine River is the only outlet to the ocean. The smolts migrate to the outlet from early May to early June.

Testing Apparatus and Procedure. Smolts were trapped at the north end of the Nilkitkwa Lake section of Babine Lake, about 100 m from the outlet of the lake. In 1980, smolts were collected from the trap on the morning after their capture; in 1981 they were collected on the evening of their capture. All smolts were trans-

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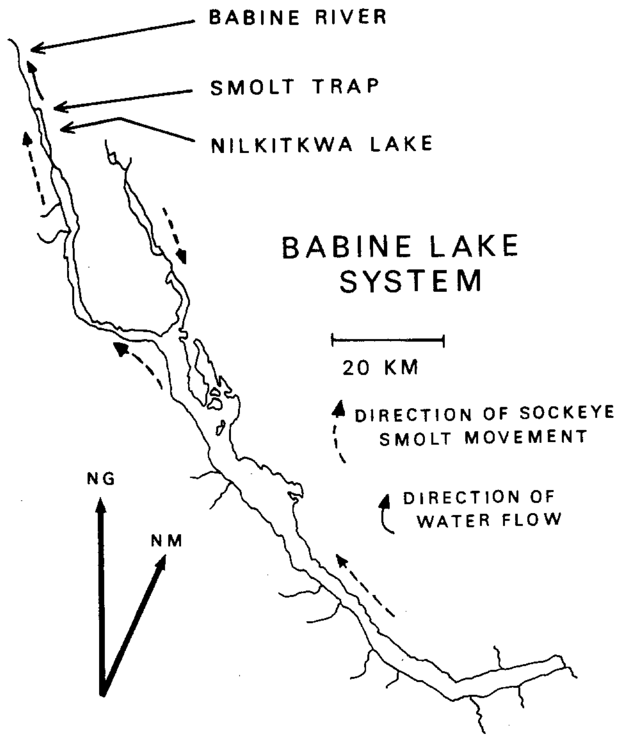

Fig. 1. Map of the Babine Lake system showing the general patterns of smolt migration and water flow. *NG* and *NM* refer to the geographic and magnetic north axes, respectively (declination = 26°)

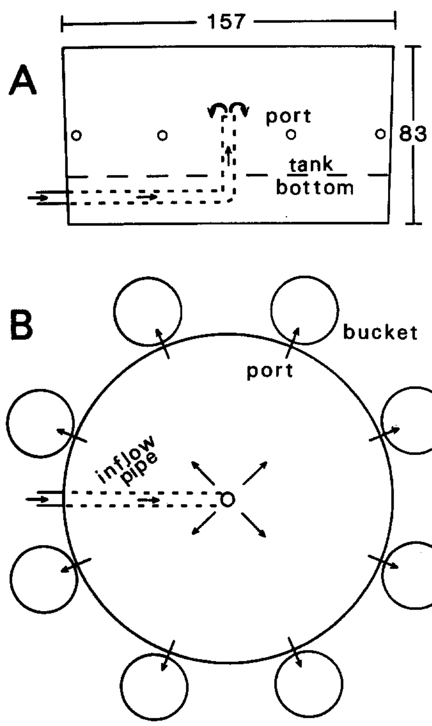

Fig. 2 A, B. Diagram of the sockeye smolt testing arena, drawn to scale (cube coil not shown). All measurements are in cm, *arrows* indicate direction of water flow. **A** Side view, buckets not shown. **B** Top view showing buckets

ported about 1 km downstream by boat to the testing site. Smolts were tested in two 1.5 m diameter circular fiberglass tanks (Fig. 2). Each tank had eight evenly spaced 4.2 cm round holes, 20 cm above the bottom. A pump in the river delivered 72 l/min in 1980 and 80 l/min in 1981 to each tank via a 5 cm PVC plastic pipe extending 27 cm up from the bottom in the center of the tank. The water mushroomed out of the pipe and flowed radially to the 8 ports. Buckets with overflow screens were placed under the ports. Smolts swimming downstream out the ports (appropriate behavior for outmigration) were caught in the buckets, counted, and then released into the river.

The tanks were placed inside identical cube coils (Rubens 1945; Quinn 1980), 2.13 m across. When connected to a DC power supply, the coil rotated the horizontal vector of the magnetic field 90° counterclockwise, putting north in the west, without substantially affecting the field's intensity or inclination. Based on compass sightings on these coils and gauss meter measurements on smaller coils, the field was very uniform at the surface of the water. At the very bottom of the tank, the field was slightly non-uniform, due to interactions between the natural and applied fields. Details on the performance of the coils may be found in Rubens (1945). Each day, one coil was activated and the other was disconnected, serving as control. The order was alternated daily during the 20 days of testing in 1980 and 21 in 1981.

The basic testing procedure was as follows. The tank was half-filled (10 cm) with water and several hundred smolts were placed in the tank with no water flow for 5 min. (The number of fish was estimated gravimetrically before each test in 1980; in 1981 all fish were counted at the end of the test). During this period, any dead or injured fish were removed. The water was then turned on, and in about 3 min water was flowing out the ports. In 1980, smolts were put into the uncovered tanks at about 0830 (Pacific Standard Time). The buckets were checked every 2 h from 0900 to 2300, and again at 0700 the next morning. The tanks were then drained, cleaned, and readied for the next group of fish. The fish could leave the tanks at any time of the day or night (except for the brief period between 07:00 and 08:30 h).

In 1981 the protocol was modified in two significant ways. First, the smolts were brought down to the tanks on the evening that they entered the smolt trap (approximately 22:00 h), rather than the next morning, in order to increase the proportion of test fish leaving the tanks. The buckets were censused early the next morning. Second, smolts were transported from the trap to the testing site in covered containers and were tested under opaque black plastic covers to prevent visual orientation.

Statistical Analysis. The 1980 data were analysed in two ways. First, the numbers of fish trapped in buckets in the 8 compass directions (360°, 45°, 90°, 135°, 180°, 225°, 270°, 315°) were tallied and a mean bearing and Rayleigh statistic for significance of the mean were calculated for each test condition (Batschelet 1965). The two test conditions were also compared using the Watson-Williams test (Schmidt-Koenig 1975). However, these procedures treat the fish as independent data points, which they are not. Therefore, Hotelling's second-order tests were used (Batschelet 1978). These tests treat each day of testing as a single data point, yielding a mean and a factor for concentration around the mean. However, the requirement that equal numbers comprise each second-order sample was not met. A high concentration of a small number of fish was weighted the same as a high concentration of a large number of fish. The first-order (one fish = one data point) analysis does not have this problem. While both first-order and second-order analytical techniques have drawbacks, the inferences drawn from them are identical, and probably adequately represent the behavior of the fish.

In 1981, inspection of the data revealed apparently bimodal distributions in both the 'coil on' and control conditions, rendering

Table 1. The numbers of sockeye smolts trapped in 8 compass directions during 20 days of testing in 1980 in the normal magnetic field and in a field shifted 90° counterclockwise, with a view of the sky

Compass directions	Test condition	
	Normal field	Altered field
360°	252	292
315°	250	295
270°	201	288
225°	180	188
180°	110	91
135°	155	143
90°	154	197
45°	231	233
Total	1,533	1,727

the Rayleigh and Hotelling's tests invalid. Each night of testing was reduced to a mean angle. The angles were doubled (Batschelet 1965) to determine the axes of bimodality and the significance of the distributions. The doubled angles of the two test groups were then compared using the Watson-Williams test. The angles were also weighted for concentration by multiplying the sines and cosines by the nightly r values to produce corrected axes of bimodality.

Results

In 1980, 1,533 fish were trapped in the buckets in the control condition (10.7% of the 14,350 fish released, Table 1). The mean bearing of these fish, counted individually, was 342° ($r=0.17$, $P<0.001$). With the coil turned on, putting magnetic north in the west, the mean bearing of 1,727 fish (12.1% of total released) was 334° ($r=0.22$, $P<0.001$). The Watson-Williams test indicated that these two sample sets were not different ($F=2.17$, $P>0.10$).

Analysis of the second-order samples resulted in a mean bearing of 327° for the control tests (Fig. 3) and 342° for the tests in the altered field (Fig. 4). Hotelling's two-sample test indicated that there was no difference between the samples ($F=0.20$). The bearing of both sample sets, under both methods of analysis, was about 340°, roughly the direction which smolts must take as they migrate in Nilkitkwa Lake to Babine River (Fig. 1).

Since the fish could see the sky and move out of the tanks essentially all day and night, it was difficult to classify the weather conditions during the tests. However, 74% of the smolts that left the tanks did so between 21:00 and 23:00 h (Table 2), roughly the time of peak catches at the smolt trap, and with total overcast between 21:00 and 23:00 h, the smolts showed no reorientation in the altered field (8 nights, $n=608$, 18°, $r=0.31$, $P<0.001$).

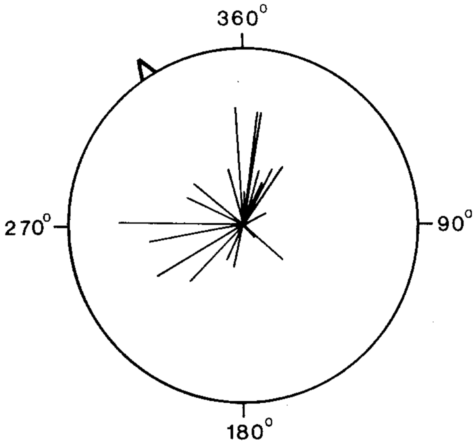

Fig. 3. Orientation of sockeye smolts tested in the normal magnetic field, with a view of the sky, in 1980. Each *line* represents the mean bearing of the smolts from one day of testing, with the length of the line directly proportional to the r statistic for that day (the radius of the circle corresponds to an r value of 0.75). *Triangle* on the perimeter: mean bearing of 327° ($n=20$, $F=4.73$, $P<0.025$)

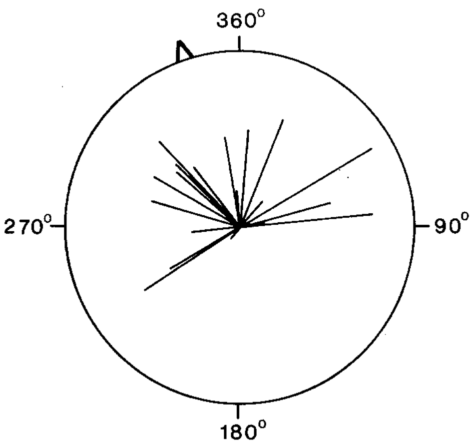

Fig. 4. Orientation of sockeye smolts tested in a magnetic field rotated 90° counterclockwise, with a view of the sky, in 1980. Each *line* represents the mean bearing of smolts from one day of testing, with the length of the line directly proportional to the r statistic for that day (the radius of the circle corresponds to an r value of 0.75). *Triangle* on the perimeter: mean bearing of 342° ($n=20$, $F=12.58$, $P<0.001$)

In 1981, 12,067 fish were released in 21 control tests and 8,219 (68.1%) were trapped in the buckets (Table 3). While in any given test the distribution of captured fish was always unimodal and almost always highly non-random, the overall distribution of first-order and second-order data was bimodal. The nightly mean angles (unweighted for concentration) were non-randomly distributed along the 341°–161° axis ($r=0.46$, $P<0.01$, Fig. 5). In the altered magnetic field, 12,023 fish were released and 7,834 (65.2%) were trapped (Table 3). Inspection indi-

Table 2. The average number of sockeye smolts moving out of the two experimental tanks in relation to the time of day (20 days of testing combined)

Time of (h) day (PST)	Average number of fish leaving both tanks (h)
07:00–11:00	4.48
11:00–13:00	3.23
13:00–15:00	0.93
15:00–17:00	0.58
17:00–19:00	0.58
19:00–21:00	2.35
21:00–23:00	60.13
23:00–07:00	1.95

Table 3. The numbers of sockeye smolts trapped in 8 compass directions during 21 days of testing in 1981 in the normal magnetic field and in a field shifted 90° counterclockwise, without a view of the sky

Compass directions	Test condition	
	Normal field	Altered field
360°	1,142	826
315°	1,035	910
270°	1,022	1,023
225°	1,004	902
180°	1,150	1,073
135°	1,049	1,051
90°	1,020	1,146
45°	797	903
Total	8,219	7,834

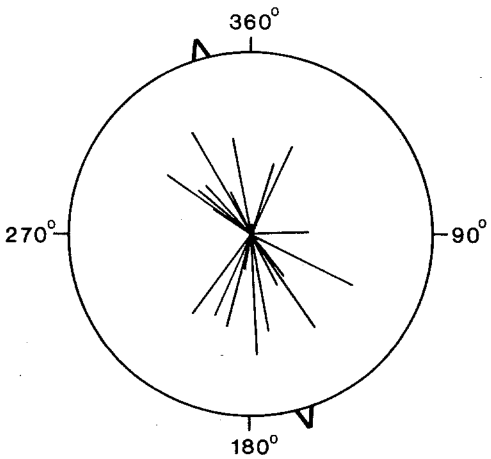

Fig. 5. Orientation of sockeye smolts tested in the normal magnetic field, under black plastic covers, in 1981. Each *line* represents the mean bearing of the smolts from one night of testing, with the length of the line directly proportional to the *r* statistic for that night (the radius of the circle corresponds to an *r* value of 0.75). *Triangles* on the perimeter: 342°–162° axis of bimodality

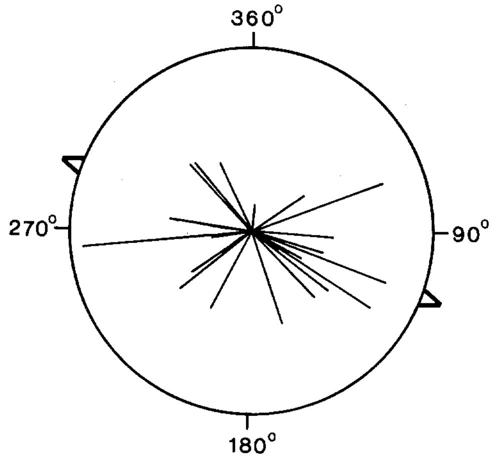

Fig. 6. Orientation of sockeye smolts tested in a magnetic field rotated 90° counterclockwise, under black plastic covers, in 1981. Each *line* represents the mean bearing of the smolts from one night of testing, with the length of the line directly proportional to the *r* statistic for that night (the radius of the circle corresponds to an *r* value of 0.75). *Triangles* on the perimeter: 286°–106° axis of bimodality

cated a bimodal distribution, and the angles were clumped along the 289° – 109° axis ($r = 0.35$, $P < 0.10$, Fig. 6). The Watson-Williams test indicated that the doubled angles in the two conditions were different ($F_{1,40} = 10.22$, $P < 0.005$). The bimodal axes calculated from the data weighted for concentration are as follows: normal field 342° – 162°, altered field 286° – 106°, difference = 56°.

Discussion

Babine Lake smolts tested under the sky in circular arenas with the opportunity to move downstream through any one of eight exits around the tank's perimeter preferred a bearing coinciding with the direction of the lake's outlet. The smolts were not affected by a change in the horizontal component of the magnetic field. It is likely that celestial cues such as the sun's position and light polarization patterns (Groot 1965) were perceived as the weather permitted during the day, and the direction of movement was established. Therefore, even total overcast at the time of movement did not force the fish to rely on magnetic cues, because the direction of movement had apparently already been selected.

In 1981, tests were conducted with the arenas covered, eliminating a view of the sky. The smolts displayed bimodal orientation, towards and away from the lake's outlet. When the magnetic field was altered, the preferred axis of orientation changed. The larger proportion of fish leaving the tanks in 1981 is attributed to the fact that they were tested on the night when they were trapped, not the next day.

Considering all the data together, four major patterns are apparent. First, the observation that smolts left the tanks shortly after dusk generally agrees with the time of peak catches at the smolt trap, and with the results of SONAR tracking studies in the lake (Groot and Wiley 1965; Groot 1972). The increase in swimming activity in the lake near dawn is not evident at the smolt trap, and was not observed in the arenas.

Second, a unimodal, outlet-directed distribution was observed in 1980 control and altered field tests. This indicates that visual orientation is of primary importance to smolts. The significance of the change from unimodal to bimodal distributions when the tanks were covered, also reported by Groot (1965), is unclear. SONAR tracking occasionally revealed reversed orientation in the lake (Groot 1972), but the experimental results may merely be artifacts of the arenas used. Interestingly, Bingman (1981) reported bimodal orientation of savannah sparrows when tested under covers.

Third, orientation of smolts under enclosed conditions was previously attributed to an unknown factor (Groot 1965). If the magnetic field was guiding such movements, a change in the field would result in a corresponding shift in orientation. The 1981 results showed a change from roughly north-south to east-west preferences with a 90° change in the horizontal component of the magnetic field when the tanks were covered, implying that the magnetic field was the guiding factor.

Although magnetic orientation can be very useful to adults and fry in open water treks, it is perhaps more critical in smolt orientation under ice. In the north country, the duration and thickness of the ice cover varies with winter temperatures and snow fall, but for most of the winter and spring the young salmon must view the sky through water covered with layers of ice and snow. In some years, the migration to the outlet begins and is accomplished under conditions of at least partial ice cover. The effects of ice on the environmental stimuli to migrate and the mechanisms guiding migration are unknown, but this would seem to be a selective force for the evolution of supplementary non-visual orientation systems in sockeye salmon.

Finally, in arriving at his conclusions on orientation patterns in Babine Lake sockeye smolts, Groot (1965) made multiple observations on a relatively small number of fish, one at a time, in round tanks with no flow. He found that the fish tended to point towards the outlet of the lake. The experimental arenas and techniques in the present study differed from Groot's in two important respects. The tanks had flowing water, and the data consisted of single observations of the movements of large numbers of fish, released in groups. Although the experimental techniques were very different, the results of the present study agree with Groot's, and validate the use of arenas for studying salmon migratory behavior.

Nocturnal orientation of sockeye salmon fry is guided chiefly by the magnetic field (Quinn 1980). However, daytime fry orientation is guided principally by celestial features, and fry only orient to the magnetic field under covers or total overcast (Quinn, in preparation). Since smolts ignored a change in the magnetic field even when the sky was overcast at the time of movement, it must be assumed that some daytime or evening celestial cue oriented them. While the work of Moore (1978) and Bingman and Able (1979) suggested that the setting sun may be an important cue for nocturnal orientation, the overhead polarization patterns occurring at dusk may also be important, as sockeye smolts can orient to polarization patterns (Groot 1965; Dill 1971). The pattern of reliance on celestial cues evident in fry and smolt studies may not persist when the salmon reach the ocean, however, as heavy cloud cover prevails on the North Pacific Ocean (Royce et al. 1968).

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