Compass orientation of sockeye salmon fry from a complex river system

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Sockeye salmon (Oncorhynchus nerka) fry from the Weaver Creek – Harrison Lake population were tested to determine whether they exhibited directional orientation in the absence of water flow. The fry oriented in a generally north-northeast direction. The presence of the moon greatly enhanced the strength of the northward orientation response, and the moon may have provided the fry with guidance information. Tests with newly emerged fry indicated little or no response to a directionally altered magnetic field. Both the passage of time and exposure to Harrison River – Harrison Lake water enhanced the compass orientation response, implying that an inherited response is triggered by environmental and temporal cues.

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Introduction

Unlike the other species of Pacific salmon which migrate to the ocean or reside in streams following emergence from gravel nests, juvenile sockeye salmon (Oncorhynchus nerka) migrate to a lake after emergence. Depending on the geography of the system, populations may have to migrate downstream, upstream, or downstream and upstream to reach their nursery lake. Brannon (1967, 1972) and Rayleigh (1967, 1971) have demonstrated that the rheotactic responses needed to reach the lakes are determined, at least in part, by genetic factors. Bodzien (1978) indicated that fry have an innate attraction to lake water in general, but that experience can modify water source preferences.

Tests in experimental tanks (Brannon 1972) indicated that sockeye fry also have compass directional preferences which may facilitate their dispersal within nursery lakes. These results were confirmed by Quinn (1980), who showed that magnetic fields play a role in guiding the fry’s orientation. However, the relative influences of innate responses and experience could not be easily determined. His principal study sites had river axes that roughly coincided with the long axes of the lakes through which the fry would disperse. Thus the compass orientation of the fry in the testing arenas could have been either an inherited lake-appropriate response or a directional preference learned from the river migration experienced prior to capture.

The questions posed in this study were (1) do newly emerged sockeye fry from a complex river system have compass directional preferences, (2) do preferences correspond to their future migration route, or are they related to their immediate experience, and (3) what environmental cues influence orientation performance?

Materials and methods

Study site

The study site was the Weaver Creek – Harrison Lake system (Fig. 1), in southwestern British Columbia, Canada, selected for the complexity it poses in fry migration. Sockeye salmon spawn in Weaver Creek, a relatively shallow rapidly flowing stream. In the spring the fry (about 3 cm long) emerge at night from gravel reds and swim down Weaver Creek and into Morris Slough which moves slowly in a southerly direction to the Harrison River. Once the fry leave the slough, within hours of emergence, they change rheotaxis, swimming up Harrison River in a northeasterly direction to finally disperse in Harrison Lake. While neither their diel pattern nor the average length of time required by the fry to make this river journey is known, some fry can be seen in the lake within 3 days of the first observed emergence from the creek.

Testing procedure

Tests were conducted between 7 and 15 May, 1979, and 26
April 4-armed absence NG showing off Release tanks (Fig. any After and experimental for cues sensory (Quinn sky NM Tests fry biases 2). IM fry 1.1980). fry night emerged night owing to the tanks or emerged to magnetic fields or structural cues, examined the fish orientation under local slow-moving sections and magnetic north axes, respectively.

April and 6 May, 1980. All fry were captured by traps on the night of their emergence. Tests were conducted outdoors in the absence of flow to eliminate the strong rheotactic behavior of migrating fry (Brannon 1972). The fry (8373 in total) were tested at night for directional preferences in three to six 4-armed wooden tanks (76 cm across) with V traps in the arms (Fig. 2). Groups of 20–40 fry were placed in the centers of the tanks in cylindrical plexiglas release devices for 5 min. Release devices were then raised and the fry allowed to move in the tanks for 45 min, at which time the arms were blocked off and traps censused to determine the direction of fish movements. The number of fish remaining in the center (21.6% overall) was also recorded. All fish were tested once, and the tanks were refilled with local water following each test. After each night of testing, the tanks were rotated to control for any biases owing to structural or visual irregularities.

Tests in 1979 were designed to characterize the orientation of fry newly emerged from the creek and to examine the sensory basis of the orientation. Use of celestial orientation cues was examined by comparing the results of tests under the sky with those conducted under black plastic covers. To test for the use of magnetic fields as an orientation cue, the experimental arena was placed inside a 112-cm cube coil (Quinn 1980). When connected to a direct current (DC) power supply, this coil generated a horizontal vector directed southwest, greater than the earth’s horizontal component. The resultant of these two vectors was a field equal in strength to the earth’s field, with the horizontal component rotated 90° counterclockwise (making magnetic north in the west) but with the same vertical component. To control for any biases in directional preference due to the coil’s presence, a second coil was built but not connected to the power supply to serve as a control. Tests were conducted with a view of the sky and under black plastic covers to examine possible interactions between celestial and magnetic guidance systems.

The 1980 series of experiments was designed to further document the initial orientation of fry from Weaver Creek and to examine the effects of time and exposure to Harrison River water on their directional preferences. Fish were tested at Weaver Creek either on the night of their capture, or after being held 7 days in the creek. Other fish were driven approximately 8 km overland (15 min) to a site on Harrison River midway between Morris Slough and Harrison Lake. Some of the latter were tested on the night of their capture, having been exposed to river water for a period of 45 min to 4 h, and others after being held in the river for 7 days. Fry were held in screen boxes placed in slow-moving sections of the streams. Wooden baffles on the sides of the boxes prevented the fish from becoming entrained to the flow direction of the creek or river.

**Statistical analysis**

Numbers of fish trapped in the north, south, east, and west arms of the tanks in each test condition were tallied and

![Diagrammatic view of the testing tank](image)
analyzed according to the Rayleigh test (with a correction for grouping, since only four directions could be chosen (Batschelet 1965)). The Watson–Williams test (Schmidt-Koenig 1975) was used to assess differences between experimental groups.

To test for possible bias owing to social interactions among the fish released as groups, the 1979 data were analyzed by calculating the bearings of fish from each release. The mean bearings calculated from these data points were very similar to the mean bearings produced by calculating each fish as a data point (Table 1, in agreement with Quinn (1980)). Since release groups were of different sizes, second-order analysis was not performed on the mean angles (Batschelet 1978), and the rest of the data were analyzed calculating each fish trapped as a data point.

**Results**

In 1979, newly emerged fry from Weaver Creek showed a northerly compass directional preference (24° overall, Table 1). The preferred direction did not correspond to the flow direction of either Weaver Creek or Morris Slough.

The mean bearing of fry released in the test arena with a view of the sky was 22°. The mean bearing of fish released in the dummy coil tests was similar (35°). The 360° bearing of fish released in the altered magnetic field was different from the coil off tests (F = 4.12, df = 1, \( P < 0.05 \)) but not different from the no coil tests (F = 1.58, df = 1, \( P > 0.10 \)). In tests under black plastic covers, the mean bearings were not different from random (\( P > 0.05 \)) in the three test conditions, but the fry were generally moving in the northeast direction (Table 1). Although the tests showed a persistent directional preference, there was no evidence that the altered magnetic field changed orientation.

Segregating the data based on the presence or absence of the moon during tests revealed that the moon apparently played a role in the orientation of the fry. Fish released under moonlit conditions (the moon was usually in the southern sky) moved north, regardless of the magnetic field condition (Table 2). However, fish released in the absence of the moon (owing either to cloud cover or the moon’s presence below the horizon) in the normal magnetic field were weakly oriented northeast, and those released in the altered magnetic field were randomly oriented. The presence of the moon accentuated directional orientation and seemed to override magnetic field changes.

The responses of fry tested at Weaver Creek in 1980 supported the findings of the previous year. While no tests were done in an altered magnetic field, fish tested in the presence of the moon showed a strong northerly preference (351°, \( r = 0.3782, P < 0.001 \), Fig. 3). In the absence of the moon, the fry were not significantly oriented, but had a weak northwest preference (Fig. 4).

To examine the influence of Harrison River water on orientation, fish were caught at Weaver Creek and briefly exposed to river water before testing. Results showed a strong north-northeast orientation in both the presence (21°, \( r = 0.3657, P < 0.001 \), Fig. 3) and absence (22°, \( r = 0.1770, P < 0.001 \), Fig. 4) of the moon. Similarly, time strengthened the orientation response. Fry held 7 days in Weaver Creek were oriented 27° (\( r = 0.0658, P < 0.05 \)) in the absence of the moon, a stronger response than had been shown by newly emerged fry. Fry held 7 days in Harrison River were oriented 346° and 356° in the presence and absence of the moon, respectively, with stronger responses under moonlight (Figs. 3 and 4). Both the passage of time and exposure to Harrison River water accentuated northerly orientation.

As in 1979, the moon’s presence was always associated with very strong northward orientation in 1980 (Fig. 4). To determine if there was a simple bias due to the light and dark areas of the tank, the data from the experimental conditions and sites were analyzed according to the moon’s position during the test. If the fish were merely moving towards the light area or away from the shadows (as was initially suspected), the mean bearing of the fish would be 180° from the moon’s position. This
TABLE 2. Orientation of sockeye salmon fry tested on the night of their capture at Weaver Creek in 1979 with a view of the sky, in the presence and absence of the moon

<table>
<thead>
<tr>
<th>Test condition</th>
<th>Moon</th>
<th>No. trapped</th>
<th>Mean angle, deg</th>
<th>Rayleigh's $r$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>No coil</td>
<td>Present</td>
<td>188</td>
<td>350</td>
<td>0.1739</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>Coil off</td>
<td>Present</td>
<td>92</td>
<td>14</td>
<td>0.1991</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Coil on</td>
<td>Present</td>
<td>110</td>
<td>360</td>
<td>0.3433</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>No coil</td>
<td>Absent</td>
<td>186</td>
<td>77</td>
<td>0.1101</td>
<td>&lt;0.20</td>
</tr>
<tr>
<td>Coil off</td>
<td>Absent</td>
<td>155</td>
<td>50</td>
<td>0.1679</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Coil on</td>
<td>Absent</td>
<td>185</td>
<td>360</td>
<td>0.0180</td>
<td>&gt;0.50</td>
</tr>
</tbody>
</table>

**WEAVER CREEK**

0 Days

![Graph](image1)

0 Days

![Graph](image2)

**HARRISON RIVER**

0 Days

![Graph](image3)

0 Days

![Graph](image4)

**Moon Present**

Fig. 3. Compass orientation of sockeye salmon fry from Weaver Creek. Fry were tested in 1980 at Weaver Creek and Harrison River on the night of their capture and 7 days later in the presence of the moon. Stippled areas are proportional to the numbers of fish trapped in those directions; arrows indicate mean bearings.

was not the case. The fish were always strongly oriented north, in spite of the changing position of the moon (Fig. 5).

To further evaluate responses to the moon, analysis of regression was performed on the moon's position (in degrees plus 180) against the mean bearing of fish tested when the moon was in that position. A slope of 1 would indicate that fry bearings changed with moon position and a slope of 0 would indicate no moon positional effect on fry bearing. The analysis resulted in a slope of $-0.11$ ($N = 4$) which was significantly different from 1 ($t = 2.93$, $P < 0.05$), but not different from 0 ($t = 0.29$). Identical conclusions were reached when the analysis used each release as a data point ($N = 69$, slope = 0.17).

**Moon Absent**

Fig. 4. Compass orientation of sockeye salmon fry from Weaver Creek. Fry were tested in 1980 at Weaver Creek and Harrison River on the night of their capture and 7 days later, in the absence of the moon. Stippled areas are proportional to the numbers of fish trapped in those directions; arrows indicate mean bearings.
compensating moon compass could be operating, evidence for moon compass orientation is only suggestive for fish (Goodyear 1973), and even with other animals evidence is scarce and sometimes equivocal (Matthews 1973; Papi and Pardi 1963; Sothibandhu and Baker 1979).

Given the very weak directional orientation of newly emerged fish at Weaver Creek in the absence of the moon, the failure to detect redirected orientation in the altered magnetic field is not surprising. Although this is the contrary to the strong responses reported by Quinn (1980) for newly emerged fry from other sockeye populations, the migratory situations were very different from Weaver Creek. In both other populations, reported orientation preferences corresponded to the direction of their lakeward migration and could serve to facilitate reaching the lakes. At Weaver Creek a strong lake-appropriate (northeast) orientation preference in newly emerged fry would tend to retard movement downstream and even concentrate fry in unsuitable feeding areas.

The change from random to oriented behavior of fish held in Weaver Creek indicates that the passage of time may be important in the orientation response pattern. This is reminiscent of Groot's (1965) evidence that sockeye smolts from the Morrison Arm of Babine Lake had a temporal shift in directional preference, as required for migration to the outlet of the lake. Exposure to Harrison Lake – Harrison River water appeared to strengthen the northerly response even without the passage of time, suggesting that odors also stimulate the orientation. Both odors and time are appropriate stimuli for this river system, because northerly orientation is not useful at least until the fish enter Harrison River.

Fry migrating out of Weaver Creek to Harrison Lake must navigate down swift and slow streams, up a slow river, change water sources and make many changes in compass direction in order to reach the nursery lake. Water flow and odors are probably the primary cues in lake-finding behavior (Bannon 1972; Bodznick 1978) and are sufficient even in this complex system to explain movement to the nursery lake. In a test arena, fry demonstrated a compass orientation roughly appropriate for movement up Harrison Lake. This may be the mechanism for dispersal away from otherwise densely occupied areas in the south end of the lake. We cannot exclude the possibility that this orientation also facilitates movement to the lake. Orientation behavior was not learned from previous experience and was heightened by the presence of the moon, time after emergence, and exposure to nursery lake water. The differing compass responses of fry from other systems indicate that this behavior is a population specific adaptation, facilitating movement along a particular migratory route.
Acknowledgements

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