INTRA-SPECIFIC DIFFERENCES IN SOCKEYE SALMON FRY COMPASS ORIENTATION MECHANISMS

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Abstract

Daytime compass orientation was studied in two populations of sockeye salmon (Oncorhynchus nerka) fry in an effort to understand the relative importance of celestial and magnetic guidance mechanisms. Both populations seemed to rely on celestial information if available, and only oriented to the magnetic field under totally overcast skies or under covers. Chilko River fry were old enough to have learned a sun compass, but fry from Weaver Creek had little if any exposure to the clear daytime sky before testing. While extremely rapid learning cannot be categorically excluded, the results indicate that sockeye salmon may possess an innate sun orientation mechanism.

It is widely accepted that animal orientation is accomplished with the aid of multiple sensory cues. However, the cues are not redundant. Young migratory birds have an innate magnetic compass which serves as a reference as they learn a stellar compass system (Wiltschko and Wiltschko, 1975, 1976). The magnetic compass is then used to select the appropriate heading for migration, and the stars are used to maintain the heading (Wiltschko and Wiltschko, 1978). Similarly, young homing pigeons use a magnetic compass to learn sun orientation (Wiltschko et al., 1981).

Sun orientation has been demonstrated in various species of fishes (Hasler et al., 1958; Hasler and Schwassmann, 1960; Schwassmann and Braemer, 1961; Schwassmann and Hasler, 1964; Winn et al., 1964; Goodyear and Ferguson, 1969; Goodyear, 1970, 1973; Loyacano et al., 1977; Goodyear and Bennett, 1979). In these fishes, the sun's time-compensated position is used as a reference for locating food or refuge from predation. The preferred compass direction is learned, and orientation is generally absent or greatly reduced when the sun is absent.

The lake migrations of juvenile sockeye salmon (Oncorhynchus nerka) are also aided by compass directional preferences (Groot, 1965; Brannon, 1972). Recent evidence indicates that this orientation ability is based on a combination of celestial and magnetic guidance mechanisms (Quinn, 1980; Quinn and Brannon, 1982). Since sockeye fry directional preferences are innate, population-specific adaptations to the geography of particular river-lake systems (Brannon, 1972; Brannon et al., 1981), these fish present an excellent opportunity to examine the developmental relationship between solar and magnetic orientation. This paper presents data on the orientation of newly emerged (0-1 day old) fry from Weaver Creek, British Columbia, and somewhat older (0-10 day old) fry from Chilko River, B.C., in order to compare the relative importance of solar and magnetic orientation in these young fish.

Methods

Test Populations

Sockeye salmon fry emerge at night from the gravel in Chilko River below Chilko Lake (Fig. 1). They generally spend 7-10 days in a quiet section of the river before swimming south, upstream to the lake where they will feed for one year before migrating to the ocean (Andrew and Geen, 1960; Brannon, 1972). However, some fry may migrate upstream as early as the day after emergence. In any case, upstream migration occurs exclusively during daylight hours. In 1979, Chilko fry were caught in the morning as they migrated up the west bank of the river towards the lake and were held in an open screen box in the river for tests that day.

In contrast to the behaviour of Chilko fry, fry from Weaver Creek emerge at night and swim downstream, usually immediately after emergence. They move down the winding creek and swim south through
Fig. 1. Map of the Chilko River - Chilko Lake system, showing water flow and direction of sockeye fry movement. NG and NM refer to the geographic and magnetic north axes (declination = 25 degrees).

Fig. 2. Map of the Weaver Creek - Harrison Lake system, showing water flow and direction of sockeye fry movement. NG and NM refer to the geographic and magnetic north axes (declination = 22.5 degrees).

Fig. 3. Compass orientation of Chilko and Weaver sockeye fry in normal and altered magnetic fields, with sky cues available (partly clear) or not available (overcast) is presented as individual fish and as pooled data from single releases.
a slow-moving slough. They then reverse rheotaxis and direction to swim northeast up Harrison River to
Harrison Lake (Fig. 2). While some fry can be seen moving up Harrison River during the day, the diel
patterns of movement in this system are not well-known. In 1981, migrating fry were caught at night
below the spawning grounds, and were held in a covered screen box for tests the next day.

Experimental Procedures

Fry directional preferences were tested in wooden 4-armed tanks, 76 cm across, with traps in the
arms (Quinn, 1980). Groups of 30-50 fry were held in a plexiglass cylinder in the center of the tank for
5 min. and then released. After 45 min., the arms of the tank were blocked off and the traps censused.
The tanks were rotated 90° after each day of testing to prevent structural irregularities from biasing
the data. The traps were interchanged after each test for the same reason. Fry were tested only once,
and the tanks were filled with fresh river water for each test.

The experiments were designed to determine the relative importance of solar and magnetic cues in
daytime orientation. Fry were tested with a view of the sky under varying conditions of overcast.
During the test, the cloud cover (0%, 25%, 50%, 75%, 100%) and the sun's presence (present, mixed, or
absent) were recorded. When wind caused rapid changes in sky conditions (especially common at Chilko
River), the presence of the sun during any portion of the test caused it to be classified as mixed.
Since light polarization patterns can be visible when the sun is behind clouds, only tests with 100%
cloud cover and the sun absent for the entire test were classified as overcast, for comparison with tests
when solar cues were available. The use of solar cues was also controlled by covering the tanks with
translucent plastic. These covers softened images considerably and distorted polarization patterns.

The role of magnetic cues was evaluated by altering the horizontal component of the field around the
tank with a 112 cm cube coil (Rubens, 1945). When activated, the coil rotated the field 90°
counter-clockwise (north into the west). The two coils used were activated or alternating days so that
the deactivated coil could serve as a control for any biases caused by the image or shadows of the frame.

The data were statistically analyzed by summing the numbers of fry trapped in the north, south, east
and west arms of the tanks and calculating the mean vector bearing and probability of randomness using
the Rayleigh test, with a correction for grouping (Batschelet, 1965; Zar, 1974). Second order mean
bearings were also calculated by treating each release as a data point, with the preferred direction
being the mean bearing of the fish trapped in that release. The relative merits of counting each fish as
a data point rather than pooling the fish in each release have been discussed by Quinn (1980) and
Brannon et al. (1981), but the overall results are similar under the two systems. Differences between
test groups were assessed using the Watson-Williams test.

Results

With a view of the sky in the normal magnetic field, Chilko River fry oriented south (Table I, II,
Fig. 3). Similar orientation was displayed in the deactivated coil and in tanks without coils (second
order analysis: F = 0.06), so the results under these conditions were combined. Southerly orientation
was displayed under both clear and overcast skies. The southerly preference was stronger under clear
and partly clear skies, but the small number of overcast releases makes comparisons unreliable. Southerly
orientation was also evident under translucent plastic covers in the normal magnetic field. When the
magnetic field was altered, fry still oriented south when permitted a view of the clear or partly clear
sky. When the sun was absent and under plastic covers, the 90° counter-clockwise change in the field was
associated with east-northeast orientation, and somewhat reduced clumping. Statistical analysis
indicated that the bearing of fry in the altered field with sky cues not available differed from the
bearings in the normal field, and the bearing in the altered field with sky cues available (Table I).

At Weaver Creek, fry in the normal magnetic field oriented northwest (with some indication of
bimodality) with a view of the clear or partly clear sky (Table III, IV, Fig. 3). They oriented
unimodally north when the sky was overcast, and north-northwest when the tanks were covered. When the
magnetic field was altered, fry with a view of the clear or partly clear sky showed west-northwest
orientation. When the sky was overcast and under covers, fry oriented southwest, 79° away from their
mean bearing in the altered field with sky cues available (Table III). Watson-Williams test of the
second order means indicated that the four conditions are not statistically similar, but exclusion of the
mean in the altered field with sky cues not available leaves the other three conditions similar (Table
III).

Discussion

When comparing the results of the Chilko River and Weaver Creek tests, three patterns are apparent.
Most obviously, the fry from these two populations oriented in roughly opposite directions (southeast vs.
northwest). This confirms the assumption that the directional preferences were population-specific,
Table I. The orientation of Chilko River fry tested in the day in 1979. The mean bearings and statistical significances were calculated using the mean of each release as a data point.

<table>
<thead>
<tr>
<th>Magnetic field</th>
<th>Sky</th>
<th>Sample size</th>
<th>Bearing</th>
<th>Rayleigh's $r$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Clear + partly clear</td>
<td>42</td>
<td>192°</td>
<td>.4522</td>
<td>&lt; .001**</td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>12</td>
<td>135°</td>
<td>.2646</td>
<td>&lt; .50</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>22</td>
<td>173°</td>
<td>.3649</td>
<td>&lt; .10</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>34</td>
<td>162°</td>
<td>.3150</td>
<td>&lt; .05</td>
</tr>
<tr>
<td>North + west</td>
<td>Clear + partly clear</td>
<td>18</td>
<td>181°</td>
<td>.7712</td>
<td>&lt; .001**</td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>6</td>
<td>112°</td>
<td>.5521</td>
<td>&lt; .20</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>12</td>
<td>17°</td>
<td>.3079</td>
<td>&lt; .50</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>18</td>
<td>61°</td>
<td>.2648</td>
<td>&lt; .50</td>
</tr>
</tbody>
</table>

* Mean bearings not statistically similar, $F = 4.45$, $P < .01$.

** Mean bearings not statistically different, $F = 0.82$, $P > .25$.

Table II. The orientation of Chilko River sockeye fry tested in the day in 1979. The numbers of fry trapped in the 4 cardinal compass directions were used to calculate the mean bearings statistical significances to the Rayleigh test.

<table>
<thead>
<tr>
<th>Magnetic field</th>
<th>Sky</th>
<th>N</th>
<th>S</th>
<th>E</th>
<th>W</th>
<th>Total</th>
<th>Bearing</th>
<th>Rayleigh's $r$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Clear + partly clear</td>
<td>246</td>
<td>527</td>
<td>299</td>
<td>322</td>
<td>1394</td>
<td>185°</td>
<td>.2246</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>109</td>
<td>161</td>
<td>122</td>
<td>72</td>
<td>464</td>
<td>136°</td>
<td>.1727</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>133</td>
<td>228</td>
<td>241</td>
<td>223</td>
<td>825</td>
<td>169°</td>
<td>.1302</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>242</td>
<td>389</td>
<td>363</td>
<td>295</td>
<td>1289</td>
<td>155°</td>
<td>.1396</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>North + west</td>
<td>Clear + partly clear</td>
<td>83</td>
<td>229</td>
<td>162</td>
<td>154</td>
<td>628</td>
<td>177°</td>
<td>.2586</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>62</td>
<td>74</td>
<td>72</td>
<td>25</td>
<td>233</td>
<td>104°</td>
<td>.2312</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>104</td>
<td>73</td>
<td>159</td>
<td>126</td>
<td>462</td>
<td>47°</td>
<td>.1089*</td>
<td>&lt; .005*</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>166</td>
<td>147</td>
<td>231</td>
<td>151</td>
<td>695</td>
<td>77°</td>
<td>.1314</td>
<td>&lt; .001</td>
</tr>
</tbody>
</table>

* $r$ value of doubled angles = .2596, $P < .001$. 

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Table III. The orientation of Weaver Creek fry tested in the day in 1981. The mean bearings and statistical significances were calculated using the mean of each release as a data point.

<table>
<thead>
<tr>
<th>Magnetic field</th>
<th>Sky</th>
<th>Sample size</th>
<th>Bearing</th>
<th>Rayleigh's r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clear + partly</td>
<td>47</td>
<td>308°</td>
<td>.0423</td>
<td>&gt; .50</td>
</tr>
<tr>
<td></td>
<td>clear</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>91</td>
<td>5°</td>
<td>.2605</td>
<td>&lt; .005</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>47</td>
<td>336°</td>
<td>.3265</td>
<td>&lt; .01</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>138</td>
<td>354°</td>
<td>.2744</td>
<td>&lt; .001* **</td>
</tr>
<tr>
<td>North + west</td>
<td>Clear + partly</td>
<td>12</td>
<td>300°</td>
<td>.4061</td>
<td>&lt; .20</td>
</tr>
<tr>
<td></td>
<td>clear</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>29</td>
<td>235°</td>
<td>.1994</td>
<td>&lt; .50</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>19</td>
<td>185°</td>
<td>.1215</td>
<td>&lt; .50</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>40</td>
<td>221°</td>
<td>.1562</td>
<td>&lt; .50</td>
</tr>
</tbody>
</table>

* Mean bearings not statistically similar, F = 5.67, P < .001.
** Mean bearings not statistically different, F = 1.45, P > .10.

Table IV. The orientation of Weaver Creek sockeye fry tested in the day in 1981. The numbers of fry trapped in the 4 cardinal compass directions were used to calculate the mean bearings and statistical significances according to the Rayleigh test.

<table>
<thead>
<tr>
<th>Magnetic field</th>
<th>Sky</th>
<th>N</th>
<th>S</th>
<th>E</th>
<th>W</th>
<th>Total</th>
<th>Bearing</th>
<th>Rayleigh's r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clear + partly</td>
<td>592</td>
<td>565</td>
<td>474</td>
<td>501</td>
<td>2132</td>
<td>315°</td>
<td>.0199</td>
<td>&gt; .50</td>
</tr>
<tr>
<td></td>
<td>clear</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>1174</td>
<td>833</td>
<td>978</td>
<td>963</td>
<td>3948</td>
<td>3°</td>
<td>.0960</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>688</td>
<td>524</td>
<td>391</td>
<td>511</td>
<td>2114</td>
<td>324°</td>
<td>.1068</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>1862</td>
<td>1357</td>
<td>1369</td>
<td>1474</td>
<td>6062</td>
<td>348°</td>
<td>.0945</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>North + west</td>
<td>Clear + partly</td>
<td>171</td>
<td>145</td>
<td>75</td>
<td>122</td>
<td>513</td>
<td>290°</td>
<td>.1163 **</td>
<td>&lt; .002**</td>
</tr>
<tr>
<td></td>
<td>clear</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Overcast</td>
<td>257</td>
<td>311</td>
<td>314</td>
<td>311</td>
<td>1193</td>
<td>177°</td>
<td>.0504</td>
<td>&lt; .05</td>
</tr>
<tr>
<td></td>
<td>Covered</td>
<td>224</td>
<td>245</td>
<td>199</td>
<td>235</td>
<td>903</td>
<td>240°</td>
<td>.0513</td>
<td>&lt; .10</td>
</tr>
<tr>
<td></td>
<td>Overcast + covered</td>
<td>481</td>
<td>556</td>
<td>513</td>
<td>546</td>
<td>2096</td>
<td>204°</td>
<td>.0434</td>
<td>&lt; .02</td>
</tr>
</tbody>
</table>

* r value of doubled angles = .0948, P < .001.
** r value of doubled angles = .2576, P < .001.
geographically appropriate behavior patterns, not artifacts of the testing arenas or procedure. Second, Weaver Creek fry orientation was weaker than that of Chilko River fry, in both the normal and altered magnetic field. Third, in both populations the magnetic field did not appear to influence orientation when the sky was at least partly clear, but under total overcast and under covers, the fry mean bearings rotated approximately 90° in the direction that the field was rotated (Fig. 3).

While the southerly orientation of Chilko River fry could have been learned during the relatively straight river migration prior to capture, the northerly preference of Weaver Creek fry could not have been learned during migration of captivity, supporting the conclusion of Brannon et al. (1981) that directional preference is an inherited characteristic. Since the rheotactic responses of sockeye fry populations are also genetically determined (Brannon, 1967, 1972), it is clear that sockeye populations are highly specialized for the geography of their incubation and rearing environments.

The difference in the strength of the orientation responses of the two populations probably reflects their different migratory patterns. Chilko River fry normally migrate in the day, and were trapped in the morning as they were swimming south. They were within 1–2 km of Chilko Lake, and were presumably fully motivated to initiate open water migration. The testing arenas simulated entrance into the lake, and fry generally moved south. Weaver Creek fry, however, normally swim down the creek at night. They must then travel south in the almost still water of the slough before ascending Harrison River to Harrison Lake. Since fry tested in the arena would normally spend several days reaching the lake, their motivation to orient in open water was probably lower than that of Chilko fry. The north-south bimodal distribution of fry with a view of the clear sky may represent the complication of southerly slough orientation and northward Harrison Lake orientation. Night-time tests also reveal a bimodal north-south preference at this site under some conditions (Quinn, unpublished data). Harrison River water (flowing from the lake) seems to stimulate northerly orientation at night (Brannon et al., 1981) and the absence of lake odors may have contributed to the weak orientation of Weaver Creek fry.

Whatever the differences in their motivational states might have been, fry from both populations oriented to the magnetic field in the absence of sky cues, but generally did not respond to a change in the field angle until 90° in the direction that both populations relied chiefly on celestial cues. While it may seem strange to regard the almost 15,000 fish as an inadequate sample size, the results should nevertheless be viewed with some caution. At Weaver Creek, the orientation in the altered field with sky cues available was not entirely coincident with that in the normal field, and a slight (but not significant) counter-clockwise deflection occurred. The generally weak orientation at this site makes comparisons somewhat unreliable. However, the results indicate that these newly emerged fish could orient to the sky. Since sockeye alevins incubate in the gravel and are negatively phototactic (Heard, 1964), the difference in the strength of orientation to the sky is not an extent prior to emergence. Some fry can be seen in the creek during the day, but they probably represent under 5% of the population. Since fry were trapped at night and were held in a covered screen box in the creek during the day, they would have had little if any opportunity to observe celestial features before testing. Moreover, the weather in 1981 was quite inclement, with several consecutive days of heavy overcast and rain. If these fry indeed learned a sun compass from such limited experience, their capacity to do so must be extraordinary (though Goodyear (1973) reported that 12-18 h old mosquitofish can orient to the sun). The alternative is that fry possess an innate time-compensating celestial compass of some sort. Based on research with fishes and other species, this would be unusual, but the possibility must be considered.

Whatever the interpretation of the Weaver Creek data, it is obvious that Chilko River fry oriented to the sky when it was clear, in spite of the altered magnetic field. This is not surprising, since most fry had been out of the gravel for a week or more. Moreover, skies in the Chilko River area tend to be clear, and were for much of the 1979 fry run. Fry were held in an open screen box, and so had ample opportunity to learn sun orientation prior to testing.

In summary, celestial cues appear to be primarily responsible for daytime sockeye fry compass orientation, but the magnetic field is used when sky cues are not available. The hypothesis that the magnetic field serves as a reference for learning celestial orientation is not supported by the results of this study, but it cannot be categorically ruled out owing to the possibility that Weaver Creek fry had seen the sun prior to testing.

Acknowledgments

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References


