Magnetic map in nonanadromous Atlantic salmon

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Long-distance migrants, including Pacific salmon (*Oncorhynchus* spp), can use geomagnetic information to navigate. We tested the hypothesis that a "magnetic map" (i.e., an ability to extract positional information from Earth's magnetic field) also exists in a population of salmon that do not undertake oceanic migrations. This study examined juvenile Atlantic salmon (*Salmo salar*) originally from a nonanadromous population in Maine transferred ∼60 years ago to a lake in central Oregon. We exposed juveniles to magnetic displacements representative of locations at the latitudinal boundaries of the Pacific salmon oceanic range in the North Pacific and at the periphery of their ancestral oceanic range in the North Atlantic. Orientation differed among the magnetic treatments, indicating that Atlantic salmon detect map information from the geomagnetic field. Despite no recent history of ocean migration, these fish displayed adaptive orientation responses similar to those observed in native Pacific salmonids. These findings indicate that use of map information from the geomagnetic field is a shared ancestral character in the family Salmonidae and is not restricted to populations with anadromous life histories. Lastly, given that Atlantic salmon are transported throughout the world for capture fisheries and aquaculture, such a robust navigational system is of some concern. Escaped individuals may have greater potential to successfully navigate, and thus invade, introduced habitats than previously suspected.

Salmo salar | orientation | navigation | migration | invasive

Long-distance migrants undertake impressive migrations that require a suite of morphological, physiological, and behavioral adaptations (1–4). Despite these specializations, the close phylogenetic relatedness between species and populations that migrate long distances and those that do not implies a high degree of flexibility in the evolution of migratory traits (1). One possible interpretation is that the remarkable abilities of migrants are simply extensions of the physiological and behavioral repertoire required for more routine movements (1, 5, 6). Nonetheless, the environmental cues animals use to direct their movement clearly differ depending on the spatial scale of the navigational task (7, 8). Although migrants and nonmigrants might be expected to use similar cues for localized movements, whether the same sensory capabilities used in long-distance migrations exist in animals with more restricted movements is less clear (1, 2).

For instance, increasing evidence shows that long-distance migrants use Earth's magnetic field as a kind of "magnetic map" (Fig. 1) to assess their location along the migratory route and orient accordingly (7, 10–18). The strength and direction of the geomagnetic field vary predictably across the globe (Fig. 1). Animals can detect total field intensity (the strength of the magnetic field), inclination angle (the angle that magnetic-field lines intersect Earth's surface) and, in some cases, declination (the difference between geographic and magnetic north) (7). Total field intensity is weakest toward the equator and becomes stronger toward the poles. Likewise, the inclination angle is parallel to Earth's surface (0°) near the equator and becomes steeper toward the magnetic poles (90°). Across much of the world, these two gradients are not entirely parallel and thus form a bicoordinate grid that allows animals to differentiate locations and have an indication of their current position relative to another magnetic target (Fig. 1) (13). Whether the magnetic maps used in long-distance navigation exist in populations that do not undertake such extraordinary movements is unknown.

Salmon are renowned for their anadromous migrations in which juveniles migrate from freshwater lakes and rivers to distant oceanic foraging grounds and then return to their natal site to spawn (19, 20). Laboratory experiments demonstrate that Pacific salmonids are capable of extracting map information from Earth's magnetic field (18, 21). Without prior migratory experience, juvenile salmon respond with oriented swimming when exposed to magnetic fields characteristic of certain regions along their oceanic migratory route (18, 21). Simulations of this behavior in ocean circulation models show it to be highly adaptive, increasing the predictability of the migratory route and facilitating movement into favorable oceanic regions (16). Although these studies were carried out on "navigationally naïve" juveniles during a nonmigratory stage of their life cycle, tested individuals belonged to populations that undertake long-distance oceanic migrations. Many salmon species also include nonanadromous populations (22, 23) and thus can serve as a valuable system for testing whether use of magnetic-map cues differs based on the life history and movement ecology of populations.

In the present study, we examined whether a nonanadromous population of Atlantic salmon can use the geomagnetic field as a map. The study population originated in Maine, but since the early 1950s, individuals from this population were spawned to

Significance

Diverse species that undertake long-distance migrations use geomagnetic "map" information to orient. Whether this is true for nonmigratory populations within these species or those migrating over considerably shorter distances is less studied. We show nonanadromous Atlantic salmon (*Salmo salar*) can extract map information from the geomagnetic field. Despite having no recent history of ocean migration and being translocated from Maine to Oregon approximately 60 years ago, juveniles exposed to magnetic fields characteristic of the North Pacific displayed adaptive orientation responses similar to those of anadromous Pacific salmonids. This navigational ability generates some concern since Atlantic salmon are transported throughout the world for aquaculture. Escaped individuals might have greater potential to successfully navigate, and thus invade, novel habitats than previously suspected.

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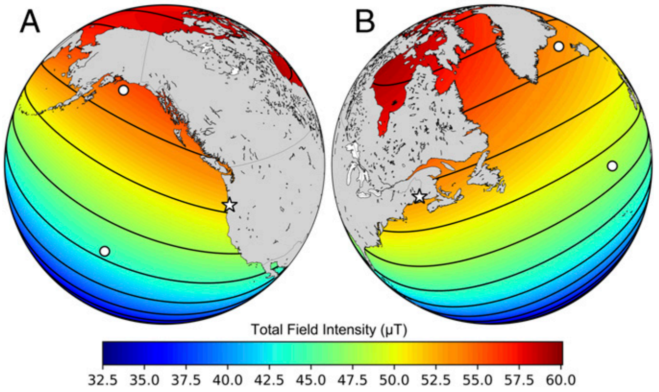

Fig. 1. Maplike information in Earth's magnetic field. (*A*) Map of total field intensity (color gradient) and inclination angle (black contour lines, 5°) across the North Pacific, based on the International Geomagnetic Reference Field (12th generation) (9). The white star indicates the rearing and testing site for experiments with juvenile Atlantic salmon. The white circles show the geographic locations of the two North Pacific test fields. (*B*) Map of the western North Atlantic, with the same magnetic conventions as in *A*. White circles indicate the geographic locations of the two North Atlantic test fields and the white star shows the ancestral home of the translocated Atlantic salmon used in this experiment.

support a recreational fishery (discontinued in 2014) within a landlocked lake in central Oregon. Microsatellite DNA analyses indicate that nonanadromous and anadromous populations in Maine are genetically distinct, likely sharing a common ancestor 8,000 to 10,000 y ago during the postglacial colonization of the region (24, 25). While we are uncertain whether this population was entirely reproductively isolated from oceanic migrants for that length of time, dams constructed in Maine rivers in the 1800s have prohibited spawning with anadromous individuals for at least 150 y (26).

Owing to their translocation to Oregon, we were able to spawn and rear this population of Atlantic salmon similarly to our earlier studies in Pacific salmonids (the same geographic location, tanks, water source, etc.) (18, 21). We used this opportunity to test whether these nonanadromous salmon, reared on the opposite coast of the North American continent, could derive positional information from Earth's magnetic field by exposing juvenile fish to "magnetic displacements" (Fig. 1). We examined orientation to the ambient field in which they were reared (as a control), two fields that exist in the North Pacific (their introduced range), and two magnetic fields that exist in the North Atlantic (their ancestral range). The experiment was designed so that (*i*) differential orientation among fields would indicate that translocated, nonanadromous salmon can use large-scale magnetic-map information to orient; (*ii*) differences in orientation between fields would show the minimum sensitivity of these salmon to magnetic-map cues; and (*iii*) the direction adopted in each field would give an indication as to whether the orientation responses are adaptive (e.g., swimming in the opposite direction of magnetic displacement) (12, 21, 27).

Results

Juvenile Atlantic salmon were exposed to one of five magnetic displacements that correspond to different geographic locations in either the North Pacific or the North Atlantic (Figs. 1 and 2). The orientation of salmon differed among these five treatments, indicating that Atlantic salmon perceive "map information" associated with the magnetic field (Mardia–Watson–Wheeler multisample test, $W = 25.9$, $P = 0.001$). Orientation significantly differed between fish tested in the northern and southern North Pacific fields (Watson's $U^2 = 0.462$, $P < 0.001$), but not between fish tested in the northern and southern North Atlantic (Watson's $U^2 = 0.111$, $P > 0.2$) (Fig. 3). Orientation differed slightly between fields in the southern North Pacific and southern North Atlantic (Watson's $U^2 = 0.188$, $P < 0.05$), but not between the northern North Pacific and northern North Atlantic magnetic fields (Watson's $U^2 = 0.107$, $P > 0.2$) (Fig. 3).

When tested in the ambient field at the Oregon rearing site, Atlantic salmon orientation was indistinguishable from a random distribution (Rayleigh $r = 0.094$, $P = 0.169$, $n = 202$), indicating that nonmagnetic factors did not strongly bias orientation. Atlantic salmon exposed to a field characteristic of the northern North Pacific oriented southward (mean heading = 170°, Rayleigh $r = 0.13$, $P = 0.018$, $n = 235$), whereas exposure to a more southern field elicited northward orientation (mean heading, 3°; Rayleigh $r = 0.14$, $P = 0.008$, $n = 238$) (Fig. 2). When exposed to magnetic fields characteristic of the North Atlantic, the juvenile salmon oriented east-southeast in a northern field (mean heading, 115°; Rayleigh $r = 0.12$, $P = 0.039$, $n = 237$) but did not display unimodal orientation to a more southern field (Rayleigh $r = 0.021$, $P = 0.898$, $n = 236$). Further examination revealed bimodal orientation along the north–south axis (mean heading, 9°/189°; Rayleigh $r = 0.12$, $P = 0.043$, $n = 236$) in response to the magnetic field existing in the southern North Atlantic (Fig. 2 and Table 1).

Discussion

While Atlantic salmon were known to be sensitive to electromagnetic fields (28, 29), our results provide evidence that they derive positional information from Earth's magnetic field for orientation. This finding suggests that the sensory capability is widespread among salmonids (18, 21) and adds to the growing and phylogenetically diverse list of animals that use a magnetic map to orient (10–15, 30, 31). The findings are consistent with previously described inherited magnetic maps in Pacific salmonids and marine turtles (16, 17). The juvenile Atlantic salmon tested had no prior migratory or navigational experience in either the Pacific Ocean or the Atlantic Ocean by which they could have learned geomagnetic field gradients. However, fish responded to magnetic displacements in the Pacific by orienting in directions that would return the fish toward favorable thermal habitat and their natal site (Fig. 2) (16).

A unique aspect of these experiments is that for many generations, the ancestors of the animals tested did not migrate to the ocean (24). As such, it does not appear that Atlantic salmon orientation is the result of natural selection to the specific oceanic conditions marked by those fields. Rather, it is likely that these salmon infer the direction of displacement from their current magnetic location by the simple rule that a stronger intensity and steeper inclination angle indicates northward displacement, whereas a weaker intensity and shallower inclination angle indicates a southward displacement (Fig. 1). Comparing Atlantic salmon orientation between the northern North Pacific and northern North Atlantic fields and between fields in the southern North Pacific and southern North Atlantic shows minimal differences, suggesting that the fish are treating fields existing in separate ocean basins similarly. This result was anticipated, given that (*i*) the large-scale magnetic map of an animal that does not undertake long-distance movements is likely to be rather general, and (*ii*) even if the map were more "finely tuned", there is no reason to presuppose that fish should adopt very different orientation in magnetic fields at the latitudinal boundaries of the North Pacific and North Atlantic. Nonetheless, orientation did slightly differ between the two southern magnetic fields (Watson's $U^2 > 0.188$, $P < 0.05$), indicating that all southern fields are not treated equivalently. This might suggest that these fish can perceive the magnitude of the displacement based on the amount of field change, but further experiments are required to confirm this possibility.

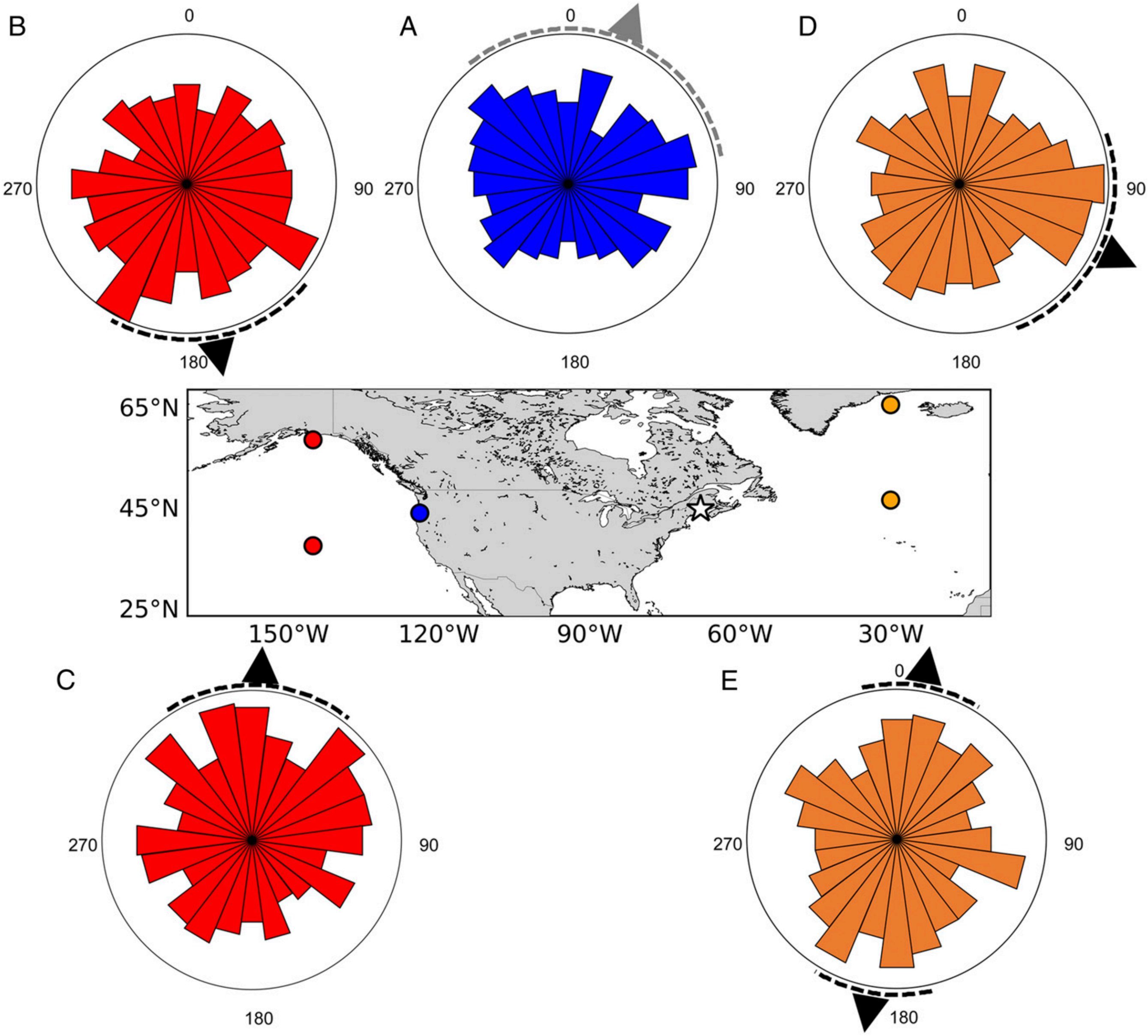

Fig. 2. Locations of magnetic fields tested and orientation histograms. (*Center*) Map of the Pacific and Atlantic oceans depicting the location of simulated magnetic fields used in the experiments (red and orange dots), the test site in Oregon (blue dot), and the ancestral location in Maine (white star). (*A–E*) Circular histograms surrounding the map show the orientation of Atlantic salmon to the ambient rearing field and simulated magnetic displacements at the northern and southern latitudinal extremes of their ocean range. The length of a wedge is proportional to the number of individuals that were oriented within that 15° interval. The distance between the center of the circle and the outer edge is scaled to 20 individuals. Outer triangles indicate the mean heading of each treatment (dashed lines indicate the 95% CI), with black coloration designating treatments in which fish were significantly oriented ($P < 0.05$) and gray coloration designating treatments that were not ($P = 0.169$). Each circle shows the orientation responses of fish to (*A*) the ambient rearing field, (*B*) a field in the northern North Pacific, (*C*) a field in the southern North Pacific, (*D*) a field in the northern North Atlantic, and (*E*) a field in the southern North Atlantic.

The implications of such a navigational system in a nonanadromous salmon population are manifold. First, it suggests that animals not undertaking extensive migratory movements can extract positional information from the magnetic field similar to orientation responses of anadromous salmonids (18, 21). Thus, magnetic sensory capabilities do not strongly differ based on the movement ecology of these organisms. Our findings bolster previous results that suggest magnetic maps might be used in local movements (30, 32), although it is unknown whether the resolution of the Atlantic salmon map is sufficient to provide positional information over the scale of a lake or river system (Figs. 1–3).

Additionally, our findings suggest potential flexibility in the navigation system of salmonids over evolutionary timescales. As connectivity is lost or reestablished between freshwater habitats and the ocean, salmon appear immediately capable of employing a magnetic map for navigating a novel environment at a broad scale. The magnetic map we have demonstrated in nonanadromous Atlantic salmon may be further modified through natural selection acting on anadromous populations to be more robust or complex (e.g., to encode distance in addition to direction, or longitude in addition to latitude) (12, 13, 15). Moreover, it seems that the magnetic environment in which fish develop modulates this

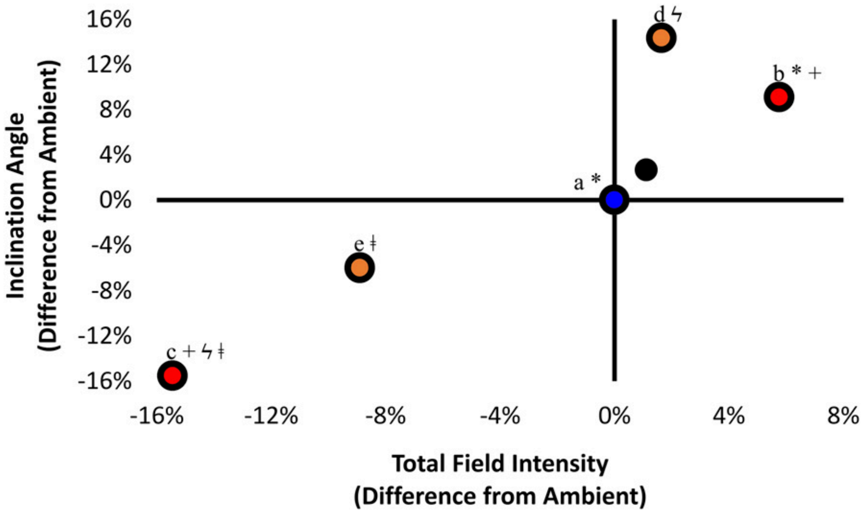

Fig. 3. Plot of total magnetic field intensity (*x* axis) versus inclination angle (*y* axis). Orange circles represent the magnetic coordinates of North Atlantic test fields. Red circles represent the magnetic coordinates of northern North Pacific test fields. The blue circle represents ambient magnetic conditions of introduced rearing location in Oregon. The black circle represents the magnetic coordinates of the ancestral home location in Maine (no fish were tested in this field). Letters correspond to those shown in Fig. 2. Orientation differed among the five treatments (Mardia–Watson–Wheeler Test, W = 25.9, $P = 0.001$). Treatments marked by the same symbol differed in pairwise comparisons of orientation (Watson's $U^2 > 0.188$, $P < 0.05$). The smallest magnetic difference between treatments that elicited different orientation was between the ambient field and the northern North Pacific field (Watson's $U^2 = 0.301$, $P < 0.01$). This result implies a minimum sensitivity to a 5.8% change in total field intensity and/or a 9.2% change in inclination angle.

inherited map (18). Future magnetic orientation experiments that focus on anadromous and nonanadromous Atlantic salmon within their native range would be beneficial to expand the scope of these findings.

Regardless, results from this study may have important implications for understanding the orientation behavior of salmonids that escape or are released from marine aquaculture facilities distant from their ancestral range. Atlantic salmon have been transported globally for commercial farming (33), including in the Northeast Pacific Ocean (34, 35). Historically, intentional introductions of anadromous populations of Atlantic salmon outside of their range were rarely successful, leading to the view that the potential for Atlantic salmon to become invasive is low (36). Nonetheless, from the late 1980s forward, fisheries across the states of Washington and Alaska and in British Columbia, Canada, have caught increasing numbers of Atlantic salmon that originated from marine net pens located in Puget Sound and along the coast of British Columbia (34). Likewise, juvenile Atlantic salmon have been found in rivers on Vancouver Island, BC, Canada (35). These observations combined with our demonstration of an adaptive magnetic map of the North Pacific (Fig. 1) may suggest a greater invasion risk than has been previously hypothesized for Atlantic salmon. Even supposing that other ecophysiological constraints keep Atlantic salmon from establishing breeding populations, the similar orientation responses of Pacific salmonids (18, 21) and translocated Atlantic salmon (Fig. 1) to magnetic fields in the North Pacific raise the possibility that competition between these species could occur in the ocean. As such, studies on how the sensory basis of navigation relates to invasion potential (31, 37) appear to be particularly relevant to salmonids (33). At present, the limited understanding of the mechanisms and sensory basis of organismal movements hinders our ability to predict species responses to novel environmental conditions (37, 38). Given the rapid pace of global climate change, anthropogenic alterations of habitats, and widespread introductions of potentially invasive species, such research deserves prioritization (39).

Methods

All experiments were conducted in accordance with Oregon State University Animal Care and Use Protocol #4394. Test subjects were descendants of a nonanadromous population from West Grand Lake in Maine (45.23°N, 67.83°W). Fish from this source population were originally translocated to Hosmer Lake in central Oregon (43.96°N, 127.78°W), and successive generations of those fish resided within the lake for at least 60 y before our testing. The likely generation time for Atlantic salmon in Hosmer Lake was about 4 y. In November 2013, 10 male and 5 female Atlantic salmon were caught at Hosmer Lake and spawned at a 2:1 ratio. Male and female gametes were transported to the Oregon Hatchery Research Center located near Alsea, OR (44.40°N, 123.75°W) and fertilized at the facility (40). The resulting progeny were incubated in standard Heath trays. Postemergence, juveniles were held in a fiberglass tank (diameter = 0.9 m) and fed a commercial pellet diet multiple times per day, following standard rearing procedures (21). Test subjects ranged from 7 to 10 cm fork length and were nearly a year old when tested (18, 21).

Table 1. Magnetic and orientation information for experimental magnetic fields

Treatment	Location	Total field intensity, μT	Inclination angle, °	Median heading, °	Mean heading, °	Rayleigh *r* (*P*)	*N*
North Pacific (northern)	59°N, 145°W	55.54	73.3	170	170	0.13 (0.018)	235
North Pacific (southern)	38°N, 145°W	44.4	56.7	355	3	0.14 (0.008)	240
North Atlantic (northern)	66°N, 30°W	53.39	76.9	105	115	0.12 (0.039)	237
North Atlantic (southern)	47°N, 30°W	47.84	63.1	5/185	9/189	0.12 (0.043)*	236
Ambient	44.4°N, 123.75°W	52.52	67.1	16	20	0.094 (0.169)	202

*Denotes significant bimodal orientation.

We filled 20 opaque circular testing arenas (diameter = 30.5 cm) to a depth of 21.5 cm with freshwater taken from the same source as that supplying the holding tanks. One fish was placed into each arena and allowed to acclimate in the still water for 10 min in the ambient magnetic field (intensity, 52.52 μT; inclination, 67.1°). After the acclimation period, the magnetic field was altered using two orthogonally arranged four-coil systems (outer vertical coil length, 3.57 m; inner horizontal coil length, 3.33 m) connected to a DC power supply located in a building adjacent to the test area (18, 21). Fish were randomly assigned to one of five treatments: (*i*) the ambient magnetic field at the test location (field intensity, 52.52 μT; inclination angle, 67.1°); (*ii*) a magnetic field at the northern periphery of Pacific salmon oceanic foraging range [55.54 μT and 73.3° (59°N, 145°W)]; (*iii*) a magnetic field at the southern periphery of Pacific salmon oceanic foraging range [44.40 μT and 56.7° (38°N, 145°W)]; (*iv*) a magnetic field at the northern periphery of Atlantic salmon oceanic foraging range [53.39 μT and 76.9° (66°N, 30°W)]; and (*v*) a magnetic field at the southern periphery of Atlantic salmon oceanic foraging range [47.81 μT and 63.0° (47°N, 30°W)]. Magnetic field values were determined by the International Geomagnetic Reference Field (11th generation) (41). The experimental magnetic fields at the test site were assessed using a triaxial fluxgate magnetometer (Applied Physics 520A). Magnetic uniformity across the experimental arenas was better than 0.4% of measurement precision. Experiments were performed outdoors from October 3–31, 2014, between 0700 and 1700 hours. Magnetic treatment groups were randomly assigned to a different time of day on a daily basis. Each fish was tested once (no repeated measures with individuals in the same field, and no fish was tested in more than one field). We draped a black mesh shade cloth (70% reduction of incident light) over the coil frames to minimize stress to the fish.

Digital images were taken at 10-s intervals during the eighth minute after a field change, and the direction of a fish's head was assessed relative to magnetic north in each of the six frames. Measurements were taken by overlaying a digital compass on the images in Microsoft PowerPoint, and headings were recorded to the nearest 5° (18, 21). We computed a mean heading for each individual that was then pooled with the others tested in the same magnetic treatment. We determined the mean heading within each treatment by calculating the mean pooled headings (the average measurement per fish) and used the Rayleigh test to determine the strength of orientation in response to a given magnetic field (42). The Mardia–Watson–Wheeler test (nonparametric) was used to determine whether orientation differed among magnetic fields. Although the Mardia–Watson–Wheeler test often is also appropriate for pairwise comparisons, it has relatively low power in cases in which distributions are bimodal (43), such as in the southern North Atlantic magnetic treatment (Fig. 2 and Table 1). Therefore, to assess whether there were differences between test fields, Watson's U^2 test (nonparametric) was applied. Data were analyzed in Oriana (v.2). Raw orientation data are provided in Dataset S1.

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