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Animal behaviour

Rearing in a distorted magnetic field disrupts the 'map sense' of juvenile steelhead trout

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We used simulated magnetic displacements to test orientation preferences of juvenile steelhead trout (*Oncorhynchus mykiss*) exposed to magnetic fields existing at the northernmost and southernmost boundaries of their oceanic range. Fish reared in natural magnetic conditions distinguished between these two fields by orienting in opposite directions, with headings that would lead fish towards marine foraging grounds. However, fish reared in a spatially distorted magnetic field failed to distinguish between the experimental fields and were randomly oriented. The non-uniform field in which fish were reared is probably typical of fields that many hatchery fish encounter due to magnetic distortions associated with the infrastructure of aquaculture. Given that the reduced navigational abilities we observed could negatively influence marine survival, homing ability and hatchery efficiency, we recommend further study on the implications of rearing salmonids in unnatural magnetic fields.

1. Introduction

An animal's navigational capacity, the process by which an animal decides when and where to move, is centrally important to its overall fitness [1]. The Earth's magnetic field is an important source of navigational information for diverse animals whose movements encompass a wide range of spatial scales [2]. In addition to providing compass information that allows animals to maintain a heading, spatial variation in magnetic parameters provides map information, from which animals can infer their location [3]. At least two components of the magnetic field are used by animals for map information, the total field intensity (strength) and inclination angle (angle which field lines intersect the surface of the Earth) [3–6]. Both components generally increase from the equator to the magnetic poles (figure 1*a*,*b*) and provide animals with latitudinal information [3,5,6,8,9]. However, the gradients are not entirely parallel and thus form a bicoordinate grid, whereby different intensity and inclination combinations can, in some cases, provide longitudinal information [10].

Recent simulated magnetic displacement experiments indicate that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) use magnetic map information to guide their migration to oceanic foraging grounds [8]. These responses appear to be inherited, given that the fish had never left the test site and did not have the opportunity to learn the large-scale magnetic gradients of the North Pacific. Environmental factors could still play an important role if fish calibrate their responses relative to the local magnetic field in which they rear. For example, the genetic programme might estimate location based on relative changes to a baseline field. Such a mechanism could be useful to mitigate problems associated with drift of the magnetic field, as the centre of the map would re-calibrate each generation [8,9].

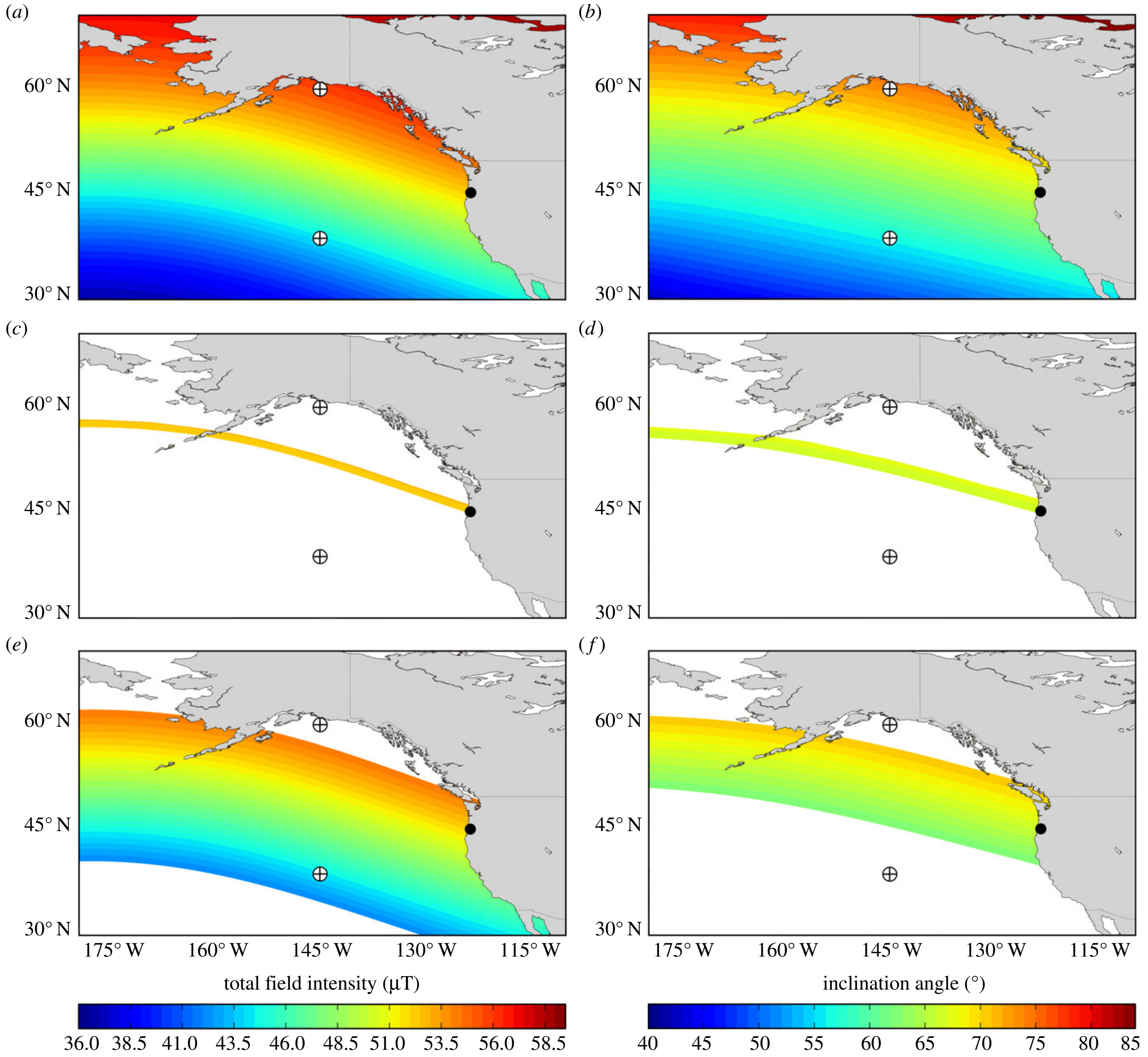

Figure 1. Gradients of (*a*) total field intensity and (*b*) inclination angle across the Northeast Pacific, based on IGRF-11 for 2014 [7]. (*c*–*f*) A geographical depiction of the magnetic gradients measured within the rearing tanks. (*c*) Intensity and (*d*) inclination gradients experienced by fish reared in the 'natural' field. (*e*) Intensity and (*f*) inclination gradients experienced by fish reared in a 'distorted' field. Black circles indicate the location of testing site. White circles with crosses show the locations of the simulated magnetic displacements.

However, problems might arise for fish exposed to magnetic fields that are uncharacteristic of the magnetic gradients across their range during the period(s) in which they acquire a baseline field, causing the internal 'magnetic map' to uncouple from geographical location. Although exposure to such fields would be rare for fish in the wild, this might be fairly common for fish produced in hatcheries, where iron pipes, concrete reinforced with steel and wires carrying electric current could greatly alter the ambient magnetic field around fish. Similar concerns have been raised over human-induced magnetic distortions for other animals that rely on the magnetic field to navigate, including sea turtles incubated in nests protected from predators by galvanized steel cages [11]. Here, we performed a series of simulated magnetic displacement experiments in which we predicted juvenile steelhead trout (*Oncorhynchus mykiss*) would orient in opposite directions: approximately southward when presented with a magnetic field that exists at the northern limit of their oceanic range and approximately northward when presented with a field at the southern limit [8]. We tested whether fish were behaviourally capable of distinguishing between these two fields when reared in either normal magnetic conditions (figure 1*c*,*d*) or distorted magnetic conditions (figure 1*e*,*f*).

2. Material and methods

Steelhead trout were taken as embryos from the ODFW Alsea Hatchery (44.423° N, 123.551° W) and transported to the Oregon Hatchery Research Center (44.404° N, 123.753° W) and incubated following routine protocol [12]. Upon hatching, one group of fish was maintained in a fibreglass tank, in which measurements of magnetic intensity ranged from 52.43 to 52.85 μT and inclination angle ranged from 65.9° to 67.8°

(figure 1*c*,*d*). A second group was maintained in a similar tank but in the vicinity of iron pipes and a concrete floor reinforced with steel rebar (typical of many hatchery conditions). In this tank, magnetic intensity ranged from 42.68 to 54.56 μT and inclination angle ranged from 62.6° to 70.7° (figure 1*e*,*f*). Fish were tested as parr, the stream-dwelling juvenile stage, at five to seven months post-fertilization.

Experiments were performed between 15 August and 12 September 2013. Skies were clear throughout testing and a mesh shade-cloth (70% reduction in incident light) was draped over the experimental apparatus to minimize stress to the fish. Twenty opaque circular buckets, each 30.5 cm in diameter and filled with still freshwater to a depth of 21.5 cm, served as orientation arenas. One fish was placed into each arena and allowed to acclimate for 10 min in the ambient magnetic field (intensity = 52.45 μT, inclination = 66.9°). The magnetic field was changed by two orthogonally arranged four-coil systems (outer, vertical coil side length = 3.315 m; inner, horizontal coil side length = 3.05 m) connected to a DC-Power supply housed in a nearby building [13]. Fish from each group were randomly assigned to either a magnetic field existing at the northern border of the oceanic range of steelhead (59° N, 145° W; intensity = 55.55 μT, inclination = 73.3°) or a magnetic field at the southern border of the range (38° N, 145° W; intensity = 444.6 μT, inclination = 56.7°) [14]. Field values were determined by the International Geomagnetic Reference Field (IGRF-11) [7] and measured with a tri-axial fluxgate magnetometer (Applied Physics 520A). A digital image of each fish was taken 8 min after the field changed and the direction the fish's head was pointing, relative to magnetic north, was recorded to the nearest 5°. The magnetic treatment groups were randomly assigned to different times on a daily basis. Individual fish were tested once. We used the Rayleigh test to test for directed orientation within each treatment group. We assessed whether fish distinguished between the two test fields (i.e. orientation differed depending on whether in a northern or southern field) using the non-parametric Mardia–Watson–Wheeler test, which calculates the probability that the distributions are identical. Comparisons were made separately for fish reared in natural and distorted magnetic conditions. Statistics were calculated in ORIANA (v. 2).

3. Results

Steelhead reared in a natural magnetic field that were exposed to the northern field oriented to the southeast, whereas those exposed to the southern field oriented to the northwest (table 1). A significant difference in orientation was observed between these two groups (Mardia–Watson–Wheeler $W_{159,160} = 17.5$, $p = 0.00016$; figure 2*a*). Conversely, fish reared in a distorted magnetic field were randomly oriented (table 1) and showed no difference between the two experimental fields (Mardia–Watson–Wheeler $W_{159,159} = 1.9$, $p = 0.387$; figure 2*b*).

4. Discussion

Without prior migratory experience, juvenile steelhead are capable of responding to magnetic fields at the latitudinal boundaries of their ocean range with oriented swimming that would lead them towards appropriate foraging grounds. This finding and similar work in Chinook salmon suggests that 'inherited magnetic maps' are a shared trait among Pacific salmonids [8]. Moreover, the similarities observed between the navigation system in juvenile salmon and

Table 1. Summary of simulated magnetic displacement results. For complete data, see electronic supplementary material.

treatment	rearing total field intensity (μT)	rearing inclination angle (°)	location of test field	test total field intensity (μT)	test inclination angle (°)	mean heading (°)	Rayleigh *R* (*p*)	*n*
normal	52.43–52.85	65.9–67.8	59°N, 145°W	55.55	73.3	139	0.175 (0.007)	160
normal	52.43–52.85	65.9–67.8	38°N, 145°W	44.46	56.7	307	0.167 (0.012)	159
distorted	42.68–54.56	62.6–70.7	59°N, 145°W;	55.55	73.3	200	0.120 (0.100)	159
distorted	42.68–54.56	62.6–70.7	38°N, 145°W	44.46	56.7	269	0.004 (0.998)	159

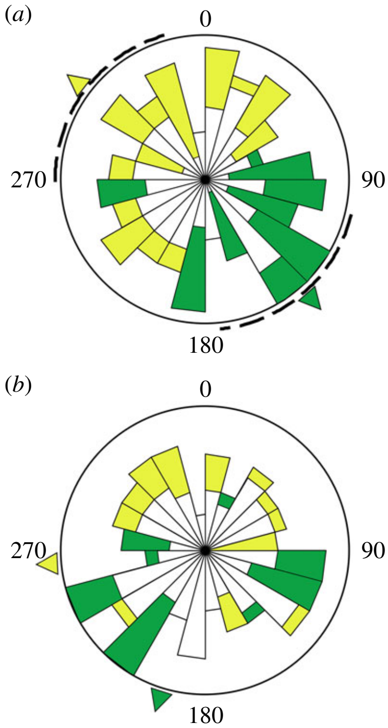

Figure 2. Circular histograms showing the orientation of steelhead to simulated magnetic displacements at the northern and southern latitudinal extremes of their ocean range. (*a*) Results for fish reared in a normal magnetic field. The green triangle indicates the mean heading of fish tested in the northern magnetic field. The yellow triangle indicates the mean heading of fish tested in the southern magnetic field. Dashed black lines indicate the 95% CI of each mean. The length of a wedge is proportional to the number of individuals that were oriented within that 15° interval. The distance between the centre of the circle and the outer edge is scaled to 12 individuals. Colours delineate the number of fish heading in a particular direction that were tested in the northern field (green) or the southern field (yellow). White coloration indicates the proportion of fish that oriented the same direction in both test fields. (*b*) Results for fish reared in a distorted magnetic field, conventions as in (*a*). The 95% CIs were not computed because fish were not significantly oriented.

hatchling sea turtles [15] suggests that this ability may underpin the life-history strategy of diverse marine migrants that exploit multiple distant oceanic regions for use as nursery habitat, foraging grounds and reproduction.

However, the results obtained using fish reared within a distorted magnetic field indicate that the 'inherited magnetic map' also has an important environmental component. Fish reared within a highly non-uniform magnetic environment failed to show appropriate orientation responses to the experimental magnetic fields. A likely explanation is that fish calibrate their magnetic map to the local field and that the inherited portion of the behaviour is an algorithm that tells fish which direction to swim if the intensity and inclination angle change a certain amount relative to the baseline field. Putting this in geographical context, fish exposed to a distorted magnetic field experienced a range of intensity and inclination angle that spans much of the typical ocean range for steelhead—from California to southwest Alaska (figure 1*e*,*f*). Fish were extremely poorly oriented in the southern magnetic field, whereas orientation was somewhat stronger and southward in the northern field (table 1). The southern field overlapped with their rearing field and the fish may not have associated the experimental field with displacement (figure 1*e*). The northern field was outside of the intensity (and inclination) range and it is possible that fish, at least partially, perceived magnetic displacement because the northern field differed from the rearing field. Further experiments are needed to clarify this possibility.

Regardless, the inability of fish reared under distorted magnetic conditions to differentiate the most extreme magnetic fields they would likely ever encounter in nature implicitly suggests that fish would be unable to use more subtle variations in the Earth's magnetic field to navigate. Whether this causes long-term problems for fish in the ocean is not known, but depends on how they construct and use their magnetic map. It is conceivable that fish frequently calibrate their magnetic maps, similar to migratory birds daily calibrating their magnetic compass [16]. If so, navigational difficulties might be short-lived. Alternatively, fish might imprint upon the local magnetic field during a critical period of development and their magnetic map might be set early on, resulting in long-tern navigational problems [17]. Given that there are a number of serious concerns in hatchery fish that could result from poor navigation abilities (e.g. high stray rates and low ocean survival [18]) and the magnetic conditions many hatchery fish experience are likely to be similar to the distortions encountered by our fish, experiments to determine how salmon construct their magnetic map are of considerable importance.

Experiments were performed in accordance with Oregon State University Animal Care and Use Protocol no. 4394.

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