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Report

An Inherited Magnetic Map Guides Ocean Navigation in Juvenile Pacific Salmon

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Summary

Migratory marine animals exploit resources in different oceanic regions at different life stages, but how they navigate to specific oceanic areas is poorly understood [1–3]. A particular challenge is explaining how juvenile animals with no prior migratory experience are able to locate specific oceanic feeding habitats that are hundreds or thousands of kilometers from their natal sites [1–7]. Although adults reproducing in the vicinity of favorable ocean currents can facilitate transport of their offspring to these habitats [7–9], variation in ocean circulation makes passive transport unreliable, and young animals probably take an active role in controlling their migratory trajectories [10–13]. Here we experimentally demonstrate that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) respond to magnetic fields like those at the latitudinal extremes of their ocean range by orienting in directions that would, in each case, lead toward their marine feeding grounds. We further show that fish use the combination of magnetic intensity and inclination angle to assess their geographic location. The "magnetic map" of salmon appears to be inherited, as the fish had no prior migratory experience. These results, paired with findings in sea turtles [12–21], imply that magnetic maps are phylogenetically widespread and likely explain the extraordinary navigational abilities evident in many long-distance underwater migrants.

Results and Discussion

Long-distance movements by marine animals play a fundamental role in ecological and evolutionary processes as well as the global economy of humans [22–25]. However, the mechanisms that underlie navigation on the ocean-basin scale remain poorly understood [1–7]. One hypothesis to explain the navigational feats of juvenile marine migrants is that they inherit orientation instructions based on spatial variation in Earth's magnetic field [13–15, 20]. Field intensity and inclination angle (the angle at which field lines intersect the earth's surface) generally increase toward the poles. The gradients of these two parameters are not parallel and thus form a kind of large-scale bicoordinate grid [26], in which different oceanic regions are delineated by different combinations of intensity and inclination [15]. In principle, animals undertaking their first long-distance migration might be guided in part by orientation responses triggered by specific regional magnetic fields [13, 14, 21]. As a convenient shorthand, we refer to this kind of navigation system as an "inherited magnetic map" because it provides animals with information about their location (i.e., positional or "map" information, in contrast to directional or "compass" information [26–28]) and is present in animals with no migratory experience (i.e., the behavior does not require animals to learn the gradient of Earth's magnetic field) [13, 20, 29]. To date, an inherited magnetic map has been demonstrated only in hatchling loggerhead sea turtles (*Caretta caretta*) from Florida (USA) [13–21]. Whether a similar system exists for any other long-distance migrant has remained controversial [4, 30–33].

Here we report that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) also have a magnetic map that facilitates navigation during their initial oceanic migration. Chinook, like other species of semelparous Pacific salmon, hatch in freshwater but migrate to sea and spend several years foraging in the ocean. They then make a single return migration to spawn in freshwater, typically in the vicinity of their natal site, and die after the breeding season [34]. Juvenile salmon use the Earth's magnetic field as a source of directional information [35, 36], but until now, evidence that salmon can also determine their geographic position from the geomagnetic field was exclusively correlative [37]. We tested Chinook salmon from the Willamette River Basin in Oregon (USA) for evidence of orientation preferences that would indicate use of an inherited magnetic map. The fish were less than one year old, had not yet embarked on their seaward migration, and remained at the testing site from hatching through experimentation (and were thus navigationally naive). We used a magnetic coil system [14, 38] to expose fish to magnetic fields that exist near the latitudinal extremes of their typical oceanic range (Table 1). If fish inherit responses to these magnetic parameters, then fish exposed to the northern field would be expected to orient approximately southward, and those exposed to the southern field would be expected to orient approximately northward [14, 16].

Fish tested in the northern magnetic field were significantly oriented toward the south-southwest (Figure 1A), and those tested in the southern magnetic field were oriented north-northeast (Figure 1C). These two distributions were significantly different (pairwise Mardia-Watson-Wheeler test, $p = 0.0003$). The orientation directions are consistent with the hypothesis that these fish have programmed responses that aid in maintaining their position within favorable foraging habitat, i.e., toward the center of their oceanic range. In contrast, the orientation of fish that were tested in the ambient local magnetic field was indistinguishable from random, ruling out the possibility that oriented swimming in the other treatments was due to nonmagnetic effects (Figure 1B).

To determine whether the observed orientation was a response to a single magnetic parameter, we presented fish with a magnetic field pairing the northern intensity with the southern inclination angle and a magnetic field pairing the

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Table 1. Test Conditions and Results of Magnetic Orientation Assays

Treatment	Location	Total Field Intensity (μT)	Inclination Angle (°)	Mean Heading	Rayleigh r	Rayleigh p	n
Ambient field	44.404°N, 123.753°W	536.9	67.2	303°	0.048	0.582	240
Northern field	59°N, 145°W	555.5	73.3	216°	0.135	0.014	233
Southern field	38°N, 145°W	444.6	56.7	17°	0.163	0.002	234
Northern intensity, southern inclination	NA	555.5	56.7	79°	0.024	0.867	240
Southern intensity, northern inclination	NA	444.6	73.3	2°	0.093	0.132	232

A multisample Mardia-Watson-Wheeler test indicates that significant differences in orientation exist among all treatments (p = 0.006). NA, not applicable.

southern intensity with the northern inclination angle. These combinations of magnetic parameters do not exist in the North Pacific and therefore should elicit a well-oriented response only if fish rely exclusively on one of the two magnetic parameters to assess their location. In these treatments, orientation was random (Figure 2), indicating that the oriented swimming in the other treatments cannot be explained as a response to only one magnetic parameter, i.e., intensity or inclination angle. This implies that the fish are using both parameters to assess their location and suggests that they use the magnetic field as a kind of bicoordinate system for ocean navigation [15, 26].

Our findings indicate that Pacific salmon are capable of responding to magnetic fields at the latitudinal boundaries of their oceanic range with oriented swimming that would lead them toward appropriate foraging grounds (Figures 1 and 3). We propose that the magnetic responses observed are inherited, because the fish tested had no migratory experience and, from hatching onward, never left the hatchery where experiments were performed. This does not imply, however, that environmental factors are unimportant; it is possible, for example, that the responses we observed are influenced by early experience with the local magnetic field. Even so, without the opportunity to learn gradients in magnetic intensity and inclination angle, the response to the change in magnetic field parameters must be inherited [14, 20]. It is particularly noteworthy that the fish tested were parr, the stream-dwelling juvenile stage [34]. Thus, it appears that the fish possess orientation responses necessary for successful ocean navigation prior to even migrating toward the sea. Given that these salmon make their oceanic migration only once, to locations where they have never been, and without the benefit of following experienced migrants, a navigation system based on inherited instructions is likely to be highly adaptive and possibly necessary [1, 5, 6, 42]. Furthermore, the magnetic orientation instructions that juveniles inherit to magnetic fields corresponding to broad oceanic regions (Figure 3) may serve as the building blocks for the subsequent and more sophisticated navigation that is hypothesized to allow these animals

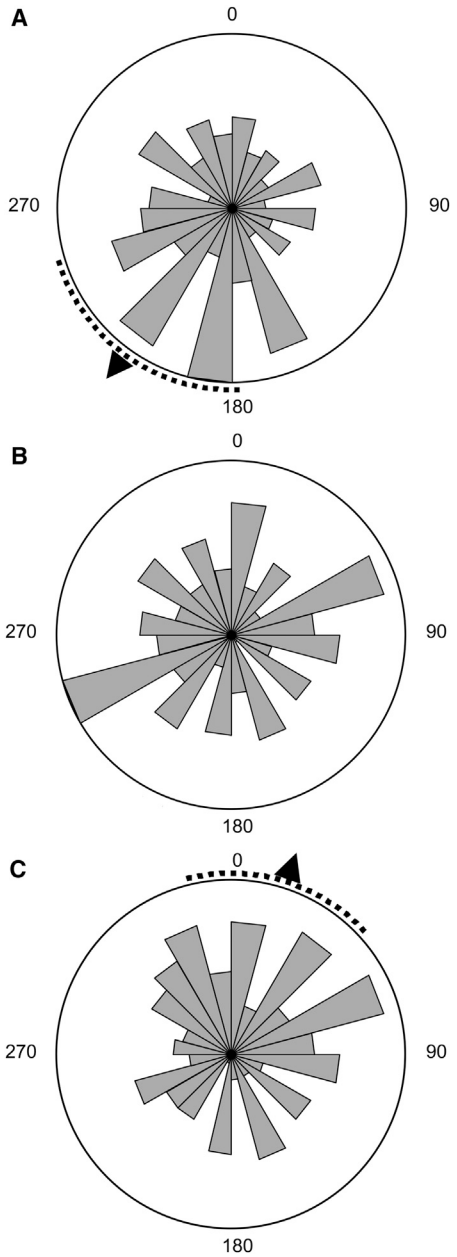

Figure 1. Orientation of Chinook Salmon to Magnetic Fields in the North Pacific

Circular histograms showing the orientation of juvenile Chinook salmon when presented with magnetic fields that exist in the northeastern Pacific Ocean. Magnetic north = 0°; length of gray bars indicates the number of fish that were oriented within each 15° range of directions. The circle edge is scaled to 21 individuals. The black triangle indicates the mean heading of each group; the dotted line on the outside of the circle represents the 95% confidence interval of the mean (shown for distributions that were significantly oriented). See Figure 3 for locations.

(A) Fish tested in a magnetic field that exists at the northern periphery of their oceanic range were oriented to the south-southwest (mean heading = 216°, Rayleigh r = 0.135, Rayleigh p = 0.014, n = 233).

(B) Orientation of fish tested in the ambient magnetic field at the testing location could not be distinguished from random (Rayleigh r = 0.048, Rayleigh p = 0.582, n = 240).

(C) Fish tested in a magnetic field that exists at the southern periphery of their oceanic range were oriented to the north-northeast (mean heading = 17°, Rayleigh r = 0.163. Rayleigh p = 0.002, n = 234).

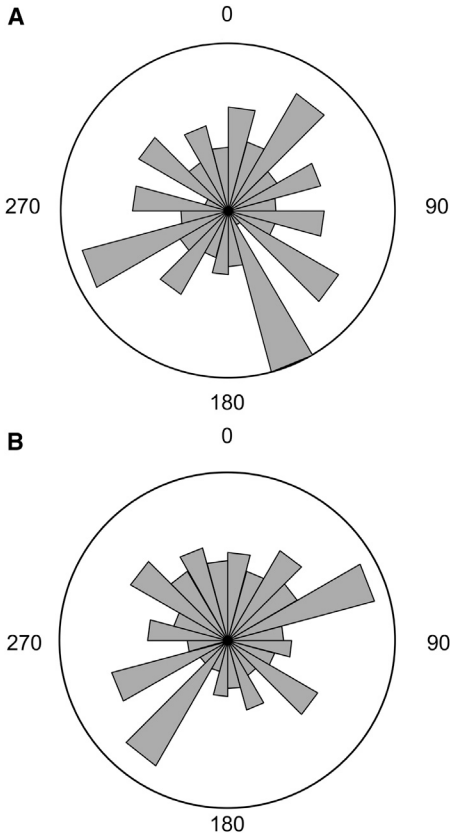

Figure 2. Orientation of Chinook Salmon to Conflicting Magnetic Cues

Circular histograms showing the orientation of juvenile Chinook salmon when presented with magnetic fields with contradictory magnetic information (conventions as in Figure 1). In both treatments, fish orientation could not be distinguished from random, indicating that orientation responses are not attributable to only one magnetic parameter.

(A) Orientation to the northern intensity and southern inclination angle (Rayleigh r = 0.024, Rayleigh p = 0.867, n = 240).

(B) Orientation to the southern intensity and northern inclination angle (Rayleigh r = 0.093, Rayleigh p = 0.132, n = 232).

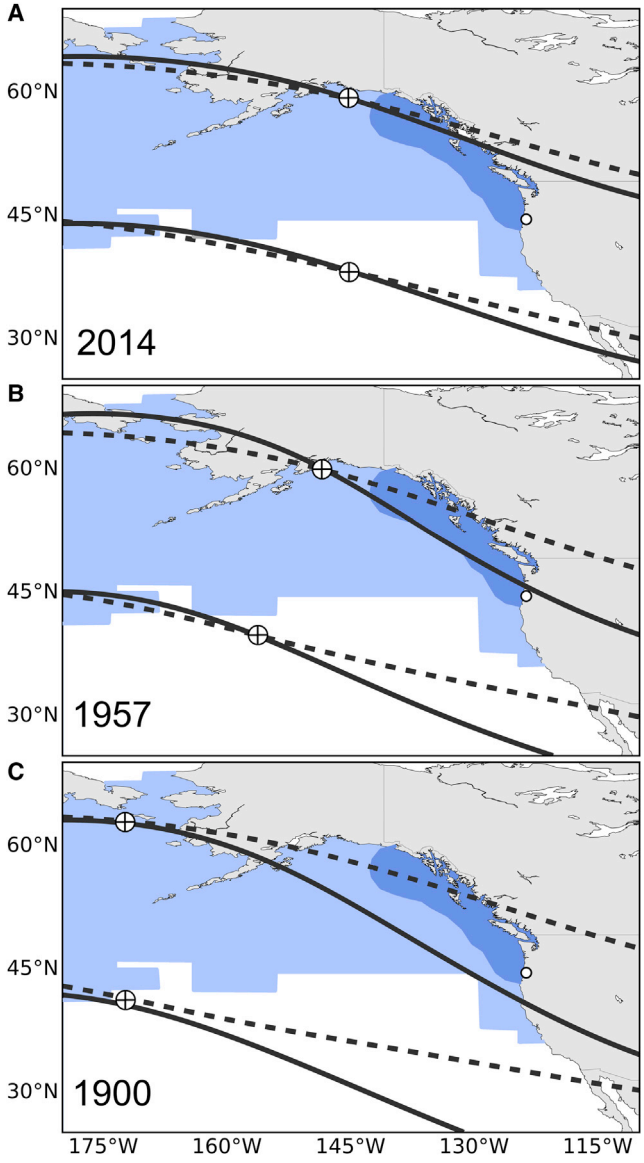

Figure 3. Locations in the Northeast Pacific Ocean Used in Simulated Magnetic Displacements

Maps show the test location (white circle) and the isolines of magnetic intensity and inclination angles presented during experiments, relative to the oceanic range of Chinook salmon. The actual range of the Chinook used in our study is unknown, but it is probably more widespread than the area where Chinook from Oregon are caught by commercial and sport fisherman (dark blue shading) [39] and less extensive than the full range of the species (light blue shading) [40]. Solid isodynamics indicate the northern and southern intensity used in experiments (555.5 μT and 444.6 μT, respectively). Dashed isoclinics indicate the northern and southern inclination angle (73.3° and 56.7°, respectively). Circles with crosses show the intersection of these two coordinates in 2014 (A), 1957 (B), and 1900 (C). Though intensity has drifted considerably (e.g., from 1940 to present, the northern intensity isodynamic is north of the test site, whereas prior to 1940, this value existed both to the north and south of the test site), the pairings of magnetic inclination angle and intensity that we presented to fish have existed in the vicinity of the latitudinal extremes of the oceanic range of Chinook for more than a century. Thus, observed orientation responses to the intensity and inclination angle pairings (Figure 1) appear to be adaptive given recent rates of field drift. Map projection is cylindrical equidistant; magnetic data are based on IGRF-11 [41].

to return with precision to their natal site for reproduction [37, 43–45].

Results also suggest that the navigation of salmon plays an important role in determining their oceanic distribution [5, 34]. Different Chinook salmon populations vary in their oceanic distributions, even if the fish enter the ocean at the same location [39, 46]. The migratory instructions that determine distributions appear to be under genetic control: two populations and their hybrids reared under identical conditions differed in distribution, and hybrids displayed an intermediate oceanic distribution relative to the two pure populations [47]. Thus, differential orientation to regional magnetic fields is a possible mechanism by which stocks segregate into broad oceanic areas [42]. Further testing the specificity and limits of the inherited magnetic map of juvenile salmon in combination with simulations of this behavior within an ocean circulation model may be a powerful way to accurately predict their at-sea movement and distribution [12, 42, 48]. Such information could have transformative influence on fisheries management.

The challenges of long-distance oceanic navigation are considerable [49], especially when compared to terrestrial navigation [2]. For instance, migratory songbirds making their

first migration to a distant, unknown site inherit a simple program in which they maintain a fixed compass course for a set duration of time that leads them, approximately, to their goal [50]. Although birds can be deflected by winds while migrating, they often mitigate drift by maintaining visual contact with the ground and by landing when conditions are adverse [51, 52]. Oceanic migrants, however, are continuously susceptible to the influence of currents. They lack stationary visual references against which current drift can be gauged and cannot "land" when conditions are unfavorable. Thus, the clock-and-compass mechanism used by many birds during their first migration is unlikely to be viable for migrants in the open ocean [2] and indeed is inadequate to explain the distribution of juvenile Chinook salmon during the early stages of their ocean migration [42].

Marine animals such as tunas, eels, sharks, sea turtles, salmon, penguins, seals, whales, and many others are capable of navigating long stretches of open ocean and can accommodate drift induced by ocean currents and correct for errors that inevitably arise [2, 3]. We suggest that the use of a large-scale magnetic map might support the successful life history of many marine migrants, allowing them to make efficient use of the spatiotemporal variability in ocean productivity and facilitating ontogenetic shifts in habitat utilization to exploit the environments that are best suited for different life stages. Given that such navigational systems have now been reported in two phylogenetically distant taxa (sea turtles and salmon), it appears likely that similar navigational systems also exist in other marine species with similar life-history patterns. Presumably the same strong selective pressure that has led to the convergent evolution of an inherited magnetic map in salmon and sea turtles permits its maintenance in the face of geomagnetic drift [15, 43] (Figure 3). Moreover, positional information inherent in Earth's magnetic field appears likely to provide an important source of navigational information for diverse animals that migrate, home, or wander over a wide range of spatial scales [53–58]. Further investigations into the behavioral, ecological, and evolutionary implications of this ability are likely to be fruitful [37, 42–45, 59].

Experimental Procedures

All experiments were conducted in accordance with Oregon State University Animal Care and Use Protocol #4394. Fish tested were the offspring of adult Chinook salmon (12 pairs) from the North Santiam River (Oregon, USA) hatchery program, spawned on September 19, 2012. Fertilized eggs were incubated at the McKenzie Hatchery and were delivered at the eyed stage to the Oregon Hatchery Research Center on November 1, 2012, where they were incubated in standard Heath trays. After emergence, juveniles were maintained in a 0.9 m diameter tank and fed a commercial pellet diet several times daily. Fish ranged from 5 to 10 cm in length at testing. Within the rearing tank, magnetic intensity was 526 μT (±0.5%) and inclination angle was 67.0° (±1.5%).

Fourteen 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, after which 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 (~50 m distant) [38]. Fish were randomly assigned to one of five treatments: (1) the ambient magnetic field at the test location, (2) a magnetic field characteristic of the northern border of the oceanic range of Chinook salmon, (3) a magnetic field characteristic of the southern border of the range, (4) a magnetic field pairing the northern intensity with the southern inclination angle, and (5) a magnetic field pairing the southern intensity with the northern inclination angle. The northern and southern magnetic fields were determined by the International Geomagnetic Reference Field (IGRF-11) [41]. The ambient field was measured at the testing site with a triaxial fluxgate magnetometer (Applied Physics 520A). Field uniformity was better than ±1% across the testing area, and no magnetic gradients were detected within the individual arenas. A digital image of each fish was taken 8 min after the field changed, and the direction that the fish's head was pointing, relative to magnetic north, was recorded to the nearest 5° by assistants unaware of the experimental predictions. Measurements were taken by overlaying a compass over the images in Microsoft PowerPoint. Experiments were performed outdoors from June 21 to July 15, 2013 between 0730 and 1700 hr. The magnetic treatment groups were randomly assigned to different times on a daily basis. Each fish was tested only once (there were no repeated measures with individuals in the same field, and no fish was tested in more than one field). A black mesh shade cloth (70% reduction in incident light) was draped over the coil frames to minimize stress to the fish; cloud cover was minimal throughout testing and solar cues likely remained visible.

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