© 2020. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2020) 223, jeb218735. doi:10.1242/jeb.218735

SHORT COMMUNICATION

A sense of place: pink salmon use a magnetic map for orientation

Nathan F. Putman[1,]*, **Chase R. Williams**[2], **Evan P. Gallagher**[2] **and Andrew H. Dittman**[3]

ABSTRACT

The use of 'map-like' information from the Earth's magnetic field for orientation has been shown in diverse taxa, but questions remain regarding the function of such maps. We used a 'magnetic displacement' experiment to demonstrate that juvenile pink salmon (*Oncorhynchus gorbuscha*) use magnetic cues to orient. The experiment was designed to simultaneously explore whether their magnetic map is used to direct fish (i) homeward, (ii) toward the center of their broad oceanic range or (iii) along their oceanic migratory route. The headings adopted by these navigationally naive fish coincided remarkably well with the direction of the juveniles' migration inferred from historical tagging and catch data. This suggests that the large-scale movements of pink salmon across the North Pacific may be driven largely by their innate use of geomagnetic map cues. Key aspects of the oceanic ecology of pink salmon and other marine migrants might therefore be predicted from magnetic displacement experiments.

KEY WORDS: Migration, Dispersal, *Oncorhynchus*, Animal navigation, Movement ecology, Magnetic orientation

INTRODUCTION

Shifts in habitat are common across diverse animal species, as reproductive sites are often spatially distinct from the nursery areas of juveniles or foraging grounds of adults (Harden Jones, 1968; Dingle, 2014). Individuals moving among these locations benefit from information about their current position relative to their migratory destination (Gould and Gould, 2012; Dingle, 2014). The sensory basis of this positional (or 'map') information is especially important in movement ecology (Gould and Gould, 2012; Hays et al., 2016; Mouritsen, 2018), because understanding the environmental cues animals use to guide their movements may help predict species responses to altered habitats and changing environmental conditions (Sutherland, 1996; Secor, 2015; Putman, 2018).

Increasing evidence suggests that animals use cues from the Earth's magnetic field as a type of 'map' to assess their position and orient accordingly (Lohmann et al., 2007; Gould, 2014, 2015). Gradients of total field intensity increase from the equator to the poles, as do the angles of the magnetic field lines that intersect the Earth's surface (Lohmann et al., 2007). Across much of the globe these two gradients are not entirely parallel, and thus form a bicoordinate grid from which both latitudinal and longitudinal information can be extracted (Putman et al., 2011). For animals that can detect geographic north, declination (the angular difference between geographic and magnetic north) may also be a component of this magnetic grid (Chernetsov et al., 2017). The most compelling evidence for this ability has come from 'magnetic displacement' experiments, whereby animals are exposed to the magnetic intensity, inclination or declination that exists at a distant location, but olfactory, inertial, visual, auditory and other potential orientation cues are held constant (Gould, 2014). Thus, differences in orientation between or among treatments can be unequivocally attributed to an ability to perceive changes in the magnetic conditions, and the direction adopted by the animals gives an indication as to how this magnetic information might be used in an ecological context (Putman et al., 2017). Magnetic displacement experiments have been successfully used to show that diverse taxa derive map information from the Earth's magnetic field, including crustaceans (Boles and Lohmann, 2003), fish (Putman et al., 2014a, b; Naisbett-Jones et al., 2017; Scanlan et al., 2018), amphibians (Fischer et al., 2001; Phillips et al., 2002), reptiles (Lohmann and Lohmann, 1994, 1996; Lohmann et al., 2001, 2004, 2012; Merrill and Salmon, 2011; Fuxjager et al., 2011, 2014; Putman et al., 2011, 2015) and birds (Kishkinev et al., 2015; Chernetsov et al., 2017; Pakhomov et al., 2018).

The bulk of studies that have conclusively demonstrated that animals use magnetic maps are on marine migrants (Putman, 2018). This ability to use magnetic maps may be critical for the widespread life-history strategy among marine animals to undertake large-scale ontogenetic shifts in location; for instance, as innate sign posts for juveniles to reach nursery and foraging grounds (Lohmann et al., 2012; Naisbett-Jones et al., 2017; Taylor and Corbin, 2019) and as learned or imprinted cues for homing (Putman and Lohmann, 2008; Lohmann and Lohmann, 2019). Nonetheless, the importance and function of magnetic sensing in the migrations of marine animals continues to be controversial (Courtillot et al., 1997; Freake et al., 2006; Durif et al., 2017). Progress in resolving these controversies is hampered by practical constraints: the sensory biology of animals that spend many years traveling across thousands of kilometers of open water is difficult to experimentally evaluate (Putman et al., 2017).

Among marine migrants, salmonids represent a particularly powerful system to study magnetic navigation (Gould, 2014). Most species of anadromous salmonids spend 1–2 years in freshwater prior to migrating to the sea and remain in the open ocean for 1–5 years, with individuals in the same population and cohort returning to spawn over a range of several years (Quinn, 2018). Pink salmon, *Oncorhynchus gorbuscha* (Walbaum 1792), differ from other Pacific salmonids in that they typically spawn in freshwater near the ocean, juveniles migrate to the sea shortly after emerging from gravel nests, they spend a relatively brief period in the ocean (12–16 months) prior to returning to their natal site to spawn, and they have a strict 2 year life-cycle (Hard et al., 1996; Quinn, 2018). Compared with other salmon species, homing pink salmon appear to 'stray' more widely and frequently (Quinn, 2018), display less robust behavioral responses to olfactory cues (Ueda, 2011) and are

---

[1]LGL Ecological Research Associates, Bryan, TX 77802, USA. [2]Department of Environmental and Occupational Health Sciences, University of Washington, Seattle, WA 98195, USA. [3]Environmental and Fisheries Sciences Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA.

*Author for correspondence (nathan.putman@gmail.com)

N.F.P., 0000-0001-8485-7455; A.H.D., 0000-0002-0957-6589

Received 14 November 2019; Accepted 18 January 2020

less sensitive to changes in temperature (Clark et al., 2011). Analysis of a dataset that tracked the migratory routes of homing pink salmon for 5 decades showed that nearly 50% of the variance could be explained by gradual drift of the Earth's magnetic field, but environmental variables associated with ocean temperature, currents and olfactory cues provided no explanatory power (Putman et al., 2014c). While such findings suggest that pink salmon may rely more heavily on geomagnetic cues than other sensory information, direct evidence for sensitivity to magnetic map cues has not been obtained in this species.

Here, we used a magnetic displacement experiment to test whether juvenile pink salmon behaviorally differentiate two magnetic fields that exist at different points on their oceanic migratory route. We chose magnetic fields that exist in regions where the headings adopted by salmon would differ depending on whether they were orienting (i) homeward, (ii) toward the center of their broad oceanic range or (iii) along their oceanic migratory route (Fig. 1). Thus, the experimental design allowed us to determine whether pink salmon possess a 'magnetic map' (Lohmann et al., 2007; Gould, 2014) and to explore how that map functions in their oceanic movements.

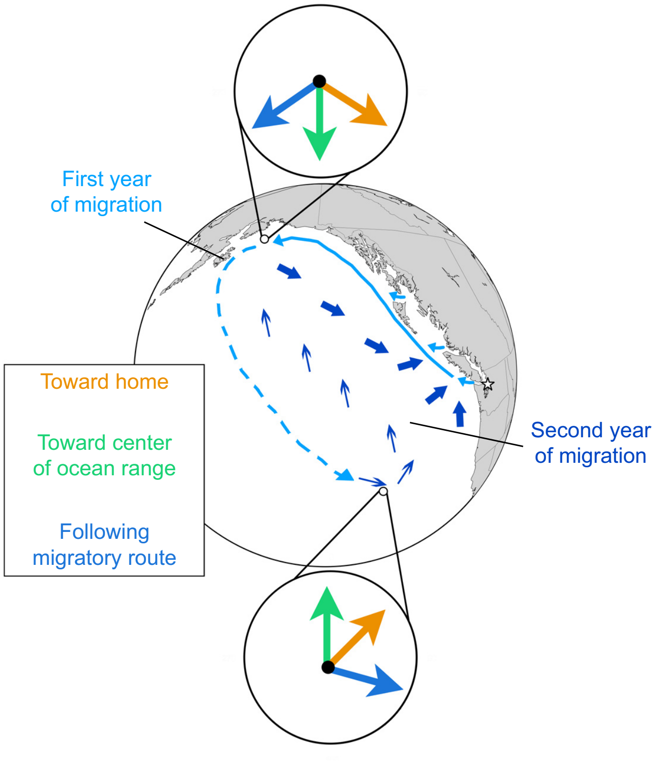

Fig. 1. Map of the hypothesized migratory route of pink salmon and possible orientation responses of juvenile pink salmon to magnetic displacements. Light blue arrows show migratory movements during the first year at sea (solid light blue indicates movements during the first spring and summer, dashed light blue indicates movements during the first autumn and winter). Dark blue arrows show hypothesized movements during the second year (thinner arrows are movements during the second spring and summer, thicker arrows are the homeward migrations during the second summer and autumn). Arrows within the circles show the direction that salmon might adopt if they use magnetic cues to assess their location and orient (i) back towards their home location (orange arrows), (ii) towards the center of their oceanic range (green arrows) or (iii) along the migratory route (blue arrows). Modified from Hard et al. (1996).

MATERIALS AND METHODS

Juvenile pink salmon were obtained from the Washington Department of Fish and Wildlife Hoodsport hatchery in Washington, USA (47.406800°N, 123.138986°W), in March 2018. Salmon were transferred to the Mukilteo Research Station of the NOAA Northwest Fisheries Science Center, Washington, USA (47.95°N, 122.302°W), for experiments. Fish were reared in indoor fiberglass tanks, plumbed with flow-through saltwater from nearby Puget Sound. Magnetic conditions across the tanks were fairly uniform [total field intensity 51.6 µT (±1.9%), inclination angle 69.3 deg (±1.7%)], though the total field intensity was somewhat reduced relative to the natural ambient field (53.67 µT, 69.37 deg). The fish were approximately 8 cm total length at the time of testing. Experiments were conducted between 06:00 h and 11:00 h, local time, from 11 to 26 August 2018.

Following protocols from prior magnetic displacement experiments (Putman et al., 2014a,b; Scanlan et al., 2018), the magnetic field was controlled using two orthogonally arranged, four-coil systems (Merritt et al., 1983) (outer, vertical coil length 3.28 m; inner, horizontal coil length 3.05 m) connected to DC power supplies located in a shelter adjacent to the test area. The frame of the coil system was covered by a shade cloth to reduce stress to the animals during the experiment and to limit access to celestial cues. Fish were tested on a platform at the center of the coils. A single fish was placed in each of the 13 opaque, cylindrical arenas (diameter 30.5 cm) filled to a depth of 21.5 cm with saltwater from the same source in which the test subjects were maintained. Prior to the placement of fish in the arenas, DC power supplies were turned on so that fish experienced the natural magnetic field associated with the geographic location of testing (intensity 53.67 µT, inclination 69.37 deg). Fish remained in this magnetic field for 10 min, after which they were exposed to one of two different magnetic fields. One of the test magnetic fields exists in the northern Gulf of Alaska (59°N, 148°W; intensity 55.2 µT, inclination=73.3 deg). The other test field exists in the southern Gulf of Alaska (43°N, 135°W; intensity 49.2 µT, inclination 63.0 deg). Field values were determined using the International Geomagnetic Reference Field (IGRF-12) (Thébault et al., 2015) and measured using a triaxial fluxgate magnetometer (FVM-400, MEDA, Inc., Dulles, VA, USA).

Beginning 8 min after the field change, cameras hanging above the test platform recorded digital images for 1 min at 10 s intervals (Scanlan et al., 2018). Thus, six images were recorded for each fish. For every image, the heading of each fish relative to magnetic north was measured using ImageJ software (US National Institutes of Health) and the mean direction was calculated for each fish. A total of 100 fish were tested, 50 fish in each of the two magnetic fields. Upon completion of the experiment, fish were killed in accordance with University of Washington Institutional Animal Care and Use Committee (IACUC) rules and approval (protocol no. 4096-1).

We pooled the mean headings of individual fish for each test field and used the Rayleigh test to measure the strength of orientation at the population level. We used the non-parametric Mardia–Watson–Wheeler test to assess whether pink salmon differentially orientated to the two test fields. Means, 95% confidence intervals and statistics were calculated using Oriana Circular Statistics v.2 (Kovach Computing Services).

RESULTS

The orientation of juvenile pink salmon exposed to northern and southern magnetic displacements significantly differed (Mardia–Watson–Wheeler test *W*=7.9, *P*=0.019), indicating that pink salmon use map information associated with the Earth's magnetic field for orientation. Salmon that were magnetically displaced to the north oriented southwestward [mean heading 213 deg, 95% confidence interval (CI) 174–253 deg, Rayleigh r=0.279, P=0.02, n=50], whereas those experiencing a magnetic displacement to the south oriented more southeastward (mean heading 109 deg, 95% CI 62–156 deg, Rayleigh r=0.236, P=0.06, n=50) (Fig. 2).

DISCUSSION

This experiment demonstrated that pink salmon perceive map information from the Earth's magnetic field and use it for orientation. The magnetic map responses do not appear to simply inform fish whether they have been displaced north or south (as inferred from similar experiments in nonanadromous salmon; Scanlan et al., 2018). Neither do the adopted headings suggest that the fish are orienting toward their home site [as in newts (Phillips et al., 2002), lobsters (Boles and Lohmann, 2003) and older sea turtles (Lohmann et al., 2004)]. Rather, the orientation adopted by fish in both test fields suggests that this behavior may be an important component of the large-scale oceanic migration of juvenile pink salmon (Figs 1 and 2). Mark–recapture and catch data (Takagi et al., 1981; Hartt and Dell, 1986; Ogura, 1994) indicate that the migratory direction of juvenile pink salmon is to the southwest in the northern Gulf of Alaska and to the southeast in the southern Gulf of Alaska (Hard et al., 1996). While the orientation patterns from tagging data reflect the movements of pink salmon several months older, these directions coincide remarkably well with the 95% CI of the mean headings of pink salmon exposed to magnetic displacements that correspond to those locations (Fig. 2). These experimental findings in juvenile pink salmon combined with a prior study examining homing routes of adult pink salmon relative to geomagnetic dynamics (Putman et al., 2014c) suggest that magnetic map cues are used to guide the entire marine migration of this species.

The use of magnetic map cues to guide migration has been observed in other species. An elaborate magnetic map that guides juvenile migration around the North Atlantic Ocean is observed in loggerhead sea turtles (*Caretta caretta*) (Lohmann et al., 2012; Putman et al., 2012, 2015). Similarly, magnetic displacement and

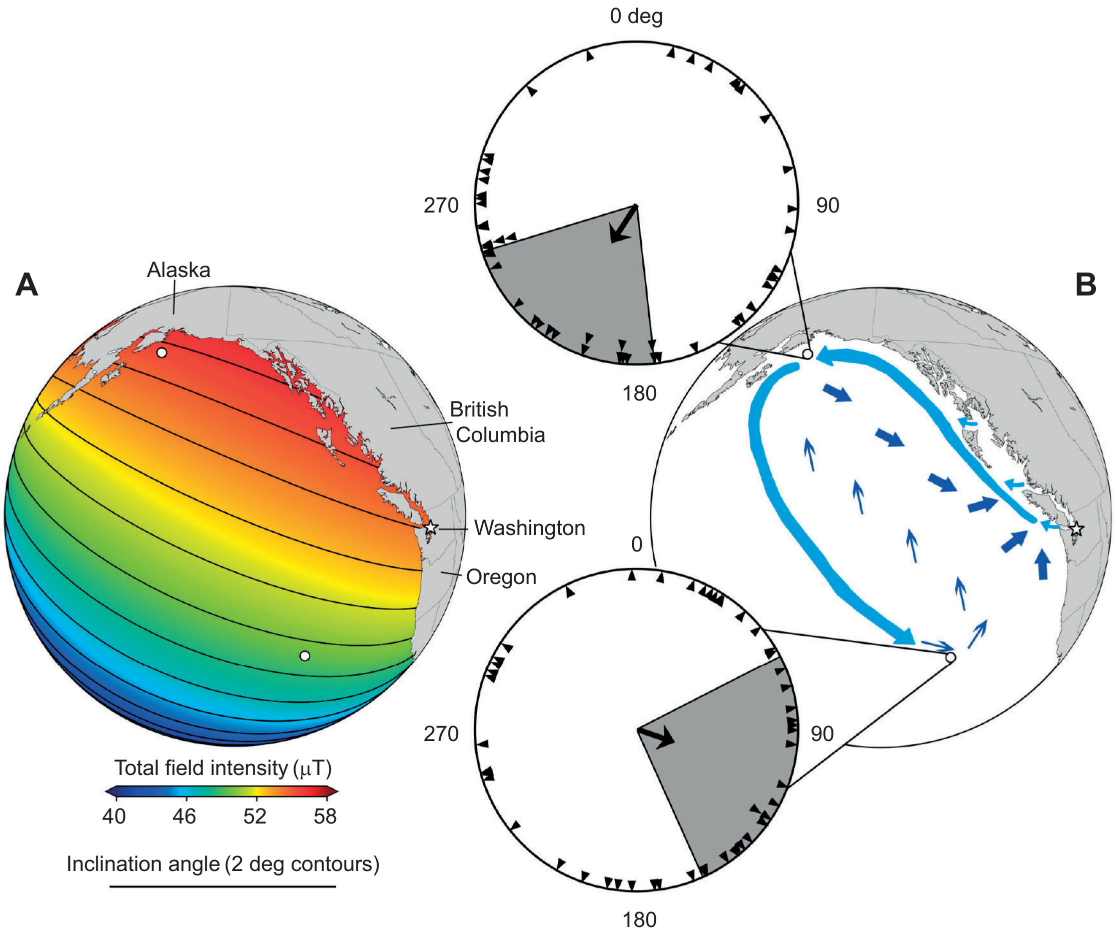

Fig. 2. Orientation of juvenile pink salmon to magnetic map information. (A) Map information available from the geomagnetic field across the northeast Pacific Ocean. Colored bands indicate total field intensity; black lines show isolines of inclination angle. The white star indicates the location where pink salmon were reared and tested. White circles indicate the locations from which magnetic values for the two magnetic displacements were obtained. Given that the gradients of intensity and inclination in this region are non-orthogonal, depending on their sensory acuity, salmon may perceive these magnetic cues as discrete points or 'swaths' extending up to a couple hundred kilometers (Putman, 2015). (B) Map of the hypothesized migratory route of pink salmon (modified from Hard et al., 1996) and juvenile pink salmon orientation in response to magnetic displacements. Light blue arrows show the migratory movements of pink salmon during their first year at sea; dark blue arrows show their hypothesized movements during the second year. Circular graphs show the orientation of juvenile pink salmon to magnetic fields that exist at the corresponding locations. Triangles show the mean heading of individuals (n=50 per magnetic field) (Table S1); the central arrow and gray shading show the population-level mean direction and 95% CI, respectively. Values are plotted relative to magnetic north (0 deg). The mean heading that juvenile pink salmon adopted in response to the magnetic displacements coincides with the direction of migration at those locations inferred from catch and tagging data (Fig. 1).

modeling experiments in European eels (*Anguilla anguilla*) indicate that their magnetic map functions to guide the juveniles' migration toward Europe (Naisbett-Jones et al., 2017). In terrestrial systems, Eurasian reed warblers (*Acrocephalus scirpaceus*) also use magnetic map cues during their seasonal migrations. Present evidence suggests that adults, but not juveniles, can correct their orientation after physical and magnetic displacements from their migratory route (Kishkinev et al., 2015; Chernetsov et al., 2017). However, the experiments to determine the role of magnetic map cues for following (rather than returning to) the migratory route have not been performed, and it is premature to conclude that juvenile birds do not also use magnetic maps.

Another important outcome of our study is the demonstration that investigations into the magnetic map sense of salmonids are robust and portable. Prior work had all been conducted in a single laboratory in Oregon and with salmon tested ∼40 km inland, in freshwater (Putman et al., 2014a,b; Scanlan et al., 2018). The present study was conducted ∼60 m from Puget Sound and in saltwater. Furthermore, it appears that pink salmon could be an excellent model species to study magnetic map orientation. As in other magnetic displacement experiments conducted with salmon, these juvenile pink salmon had no prior navigational experience by which they could have learned the geomagnetic field gradients across the Pacific Ocean. Their ability to discriminate the two test fields suggests that differential orientation to magnetic fields is innate (Putman et al., 2014a). However, we were able to show fish differentiate magnetic map cues, using a relatively small sample size (n=50 fish per treatment) relative to studies in steelhead trout (*O. mykiss*), which used 160 fish per treatment (Putman et al., 2014b), or Chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon, which used over 200 fish per treatment (Putman et al., 2014a; Scanlan et al., 2018). Likewise, the sensory ecology of pink salmon appears to favor their use of geomagnetic cues over other potential sources of information (Putman et al., 2014c) and, relative to other species of salmon, their use of olfactory cues appears reduced (Ueda, 2011).

Our present finding that spontaneous orientation of juvenile pink salmon to magnetic fields closely agrees with catch-based inferences on migratory directions (Fig. 2) lends support to the view that magnetic map cues play an important role in the ontogenetic migrations of diverse marine species (Secor, 2015; Putman, 2018). Magnetic displacement experiments paired with simulation of the observed behavior in realistic environmental models could be a powerful and relatively inexpensive way to investigate the many open questions in migration ecology (Putman, 2015; Burke et al., 2016). Such work could provide an important component of the information needed to improve predictions of shifting distributions and abundances of marine species in response to changing environmental conditions (Secor, 2015; Hays et al., 2016).

Acknowledgements

We thank William Ardren for use of his magnetometer and David Minkoff for advice on construction of the magnetic coil. We thank David Noakes, Michelle Scanlan and Amanda Pollock for constructive discussion regarding this work. We appreciate the assistance of Michael Maher, Paul McElhany, Danielle Perez, Darran May and Richard Ramsden with rearing and infrastructure at the NWFSC Mukilteo Field Station. We also thank Jorge Villarreal, Mark Cylwik and staff at the Washington Department of Fish and Wildlife's Hoodsport Hatchery for supplying pink salmon juveniles for this study. The views expressed herein are those of the authors and do not necessarily reflect the views of the University of Washington, NOAA, or any of its subagencies.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.F.P., C.R.W., E.P.G., A.H.D.; Methodology: N.F.P., C.R.W., A.H.D.; Formal analysis: N.F.P.; Investigation: C.R.W.; Resources: E.P.G., A.H.D.; Data curation: C.R.W.; Writing - original draft: N.F.P.; Writing - review & editing: N.F.P., C.R.W., E.P.G., A.H.D.; Visualization: N.F.P.; Supervision: N.F.P., A.H.D.; Project administration: E.P.G., A.H.D.; Funding acquisition: E.P.G., A.H.D.

Funding

This work was funded in part by grants from the Washington Ocean Acidification Center, the Washington Sea Grant, University of Washington program, and the NOAA Ocean Acidification Program. Additional support was provided by the NOAA Fisheries Northwest Fisheries Science Center.

References

Boles, L. C. and Lohmann, K. J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60. doi:10.1038/nature01226

Burke, B. J., Anderson, J. J., Miller, J. A., Tomaro, L., Teel, D. J., Banas, N. S. and Baptista, A. M. (2016). Estimating behavior in a black box: how coastal oceanographic dynamics influence yearling Chinook salmon marine growth and migration behaviors. *Environ. Biol. Fishes* **99**, 671-686. doi:10.1007/s10641-016-0508-7

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A. and Mouritsen, H. (2017). Migratory Eurasian reed warblers can use magnetic declination to solve the longitude problem. *Curr. Biol.* **27**, 2647-2651.e2. doi:10.1016/j.cub.2017.07.024

Clark, T. D., Jeffries, K. M., Hinch, S. G. and Farrell, A. P. (2011). Exceptional aerobic scope and cardiovascular performance of pink salmon (Oncorhynchus gorbuscha) may underlie resilience in a warming climate. *J. Exp. Biol.* **214**, 3074-3081. doi:10.1242/jeb.060517

Courtillot, V., Hulot, G., Alexandrescu, M., le Mouë, J.-L. and Kirschvink, J. L. (1997). Sensitivity and evolution of sea-turtle magnetoreception: observations, modelling and constraints from geomagnetic secular variation. *Terra Nova* **9**, 203-207. doi:10.1111/j.1365-3121.1997.tb00013.x

Dingle, H. (2014). *Migration: The Biology of Life on the Move*. USA: Oxford University Press.

Durif, C. M. F., Bonhommeau, S., Briand, C., Browman, H. I., Castonguay, M., Daverat, F., Dekker, W., Diaz, E., Hanel, R., Miller, M. J. et al. (2017). Whether European eel leptocephali use the Earth's magnetic field to guide their migration remains an open question. *Curr. Biol.* **27**, R998-R1000. doi:10.1016/j.cub.2017.08.045

Fischer, J. H., Freake, M. J., Borland, S. C. and Phillips, J. B. (2001). Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* **62**, 1-10. doi:10.1006/anbe.2000.1722

Freake, M. J., Muheim, R. and Phillips, J. B. (2006). Magnetic maps in animals: a theory comes of age? *Q. Rev. Biol.* **81**, 327-347. doi:10.1086/511528

Fuxjager, M. J., Eastwood, B. S. and Lohmann, K. J. (2011). Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. *J. Exp. Biol.* **214**, 2504-2508. doi:10.1242/jeb.055921

Fuxjager, M. J., Davidoff, K. R., Mangiamele, L. A. and Lohmann, K. J. (2014). The geomagnetic environment in which sea turtle eggs incubate affects subsequent magnetic navigation behaviour of hatchlings. *Proc. R. Soc. B* **281**, 20141218. doi:10.1098/rspb.2014.1218

Gould, J. L. (1982). The map sense of pigeons. *Nature* **296**, 205. doi:10.1038/296205a0

Gould, J. L. (2014). Animal navigation: a map for all seasons. *Curr. Biol.* **24**, R153-R155. doi:10.1016/j.cub.2014.01.030

Gould, J. L. (2015). Animal navigation: birds have magnetic maps. *Curr. Biol.* **25**, R836-R838. doi:10.1016/j.cub.2015.08.041

Gould, J. L. and Gould, C. G. (2012). *Nature's Compass: The Mystery of Animal Navigation*, Vol. 16: Princeton University Press.

Hard, J. J., Kope, R. G., Grant, W. S., Waknitz, F. W., Parker, L. T. and Waples, R. S. (1996). *Status Review of Pink Salmon from Washington, Oregon and California*. US Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-25, 131pp.

Harden Jones, F. R. (1968). *Fish Migration*. London: Arnold.

Hartt, A. C. and Dell, M. B. (1986). Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. *Int. N. Pac. Fish. Comm. Bull.* **46**, 1-105.

Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., Bailleul, F., Bowen, W. D., Caley, M. J., Costa, D. P. et al. (2016). Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* **31**, 463-475. doi:10.1016/j.tree.2016.02.015

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D. and Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Curr. Biol.* **25**, R822-R824. doi:10.1016/j.cub.2015.08.012

Lohmann, K. and Lohmann, C. (1994). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23-32.

Lohmann, K. J. and Lohmann, C. M. (1996). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59. doi:10.1038/380059a0

Lohmann, K. J. and Lohmann, C. M. F. (2019). There and back again: natal homing by magnetic navigation in sea turtles and salmon. *J. Exp. Biol.* **222** Suppl 1, jeb184077. doi:10.1242/jeb.184077

Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366. doi:10.1126/science.1064557

Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. and Swing, T. (2004). Animal behaviour: geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909-910. doi:10.1038/428909a

Lohmann, K. J., Lohmann, C. M. and Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697-3705. doi:10.1242/jeb.001313

Lohmann, K. J., Putman, N. F. and Lohmann, C. M. (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342. doi:10.1016/j.conb.2011.11.005

Merrill, M. W. and Salmon, M. (2011). Magnetic orientation by hatchling loggerhead sea turtles (Caretta caretta) from the Gulf of Mexico. *Mar. Biol.* **158**, 101-112. doi:10.1007/s00227-010-1545-y

Merritt, R., Purcell, C. and Stroink, G. (1983). Uniform magnetic field produced by three, four, and five square coils. *Rev. Sci. Instrum.* **54**, 879-882. doi:10.1063/1.1137480

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* **558**, 50-59. doi:10.1038/s41586-018-0176-1

Naisbett-Jones, L. C., Putman, N. F., Stephenson, J. F., Ladak, S. and Young, K. A. (2017). A magnetic map leads juvenile European eels to the Gulf Stream. *Curr. Biol.* **27**, 1236-1240. doi:10.1016/j.cub.2017.03.015

Ogura, M. (1994). Migratory behavior of Pacific salmon (*Oncorhynchus* spp.) in the open sea. *Bull. Natl. Res. Inst. Far Seas Fish. (Japan)* **31**, 1-139.

Pakhomov, A., Anashina, A., Heyers, D., Kobylkov, D., Mouritsen, H. and Chernetsov, N. (2018). Magnetic map navigation in a migratory songbird requires trigeminal input. *Sci. Rep.* **8**, 11975. doi:10.1038/s41598-018-30477-8

Phillips, J. B., Freake, M. J., Fischer, J. H. and Borland, C. S. (2002). Behavioral titration of a magnetic map coordinate. *J. Comp. Physiol. A* **188**, 157-160. doi:10.1007/s00359-002-0286-x

Putman, N. F. (2015). Inherited magnetic maps in salmon and the role of geomagnetic change. *Integr. Comp. Biol.* **55**, 396-405. doi:10.1093/icb/icv020

Putman, N. F. (2018). Marine migrations. *Curr. Biol.* **28**, R972-R976. doi:10.1016/j.cub.2018.07.036

Putman, N. F. and Lohmann, K. J. (2008). Compatibility of magnetic imprinting and secular variation. *Curr. Biol.* **18**, R596-R597. doi:10.1016/j.cub.2008.05.008

Putman, N. F., Endres, C. S., Lohmann, C. M. and Lohmann, K. J. (2011). Longitude perception and bicoordinate magnetic maps in sea turtles. *Curr. Biol.* **21**, 463-466. doi:10.1016/j.cub.2011.01.057

Putman, N. F., Verley, P., Shay, T. J. and Lohmann, K.J., (2012). Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *Journal of Experimental Biology*, **215**, 1863-1870. doi:10.1242/jeb.067587

Putman, N. F., Scanlan, M. M., Billman, E. J., O'Neil, J. P., Couture, R. B., Quinn, T. P., Lohmann, K. J. and Noakes, D. L. (2014a). An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr. Biol.* **24**, 446-450. doi:10.1016/j.cub.2014.01.017

Putman, N. F., Meinke, A. M. and Noakes, D. L. (2014b). Rearing in a distorted magnetic field disrupts the 'map sense' of juvenile steelhead trout. *Biol. Lett.* **10**, 20140169. doi:10.1098/rsbl.2014.0169

Putman, N. F., Jenkins, E. S., Michielsens, C. G. and Noakes, D. L. (2014c). Geomagnetic imprinting predicts spatio-temporal variation in homing migration of pink and sockeye salmon. *J. R. Soc. Interface* **11**, 20140542. doi:10.1098/rsif.2014.0542

Putman, N. F., Verley, P., Endres, C. S. and Lohmann, K. J. (2015). Magnetic navigation behavior and the oceanic ecology of young loggerhead sea turtles. *J. Exp. Biol.* **218**, 1044-1050. doi:10.1242/jeb.109975

Putman, N. F., Naisbett-Jones, L. C., Stephenson, J. F., Ladak, S. and Young, K. A. (2017). Response to Durif et al. *Curr. Biol.* **27**, R1000-R1001. doi:10.1016/j.cub.2017.08.046

Quinn, T. P. (2018). *The Behavior and Ecology of Pacific Salmon and Trout*: University of Washington Press.

Scanlan, M. M., Putman, N. F., Pollock, A. M. and Noakes, D. L. (2018). Magnetic map in nonanadromous Atlantic salmon. *Proc. Natl Acad. Sci. USA* **115**, 10995-10999. doi:10.1073/pnas.1807705115

Secor, D. H. (2015). *Migration Ecology of Marine Fishes*: JHU Press.

Sutherland, W. J. (1996). *From Individual Behaviour to Population Ecology*, Vol. 11: Oxford University Press on Demand.

Takagi, K., Aro, K. V., Hartt, A. C. and Dell, M. B. (1981). Distribution and origin of pink salmon (Oncorhynchus gorbuscha) in offshore waters of the North Pacific ocean. *Int. N. Pac. Fish. Comm. Bull.* **40**, 195.

Taylor, B. K. and Corbin, S. (2019). Bioinspired magnetoreception and navigation in nonorthogonal environments using magnetic signatures. *Bioinspir. Biomim.* **14**, 066009. doi:10.1088/1748-3190/ab40f8

Thébault, E., Finlay, C. C., Alken, P., Beggan, C. D., Canet, E., Chulliat, A., Langlais, B., Lesur, V., Lowes, F. J., Manoj, C. et al. (2015). Evaluation of candidate geomagnetic field models for IGRF-12. *Earth Planets Space* **67**, 112. doi:10.1186/s40623-015-0273-4

Ueda, H. (2011). Physiological mechanism of homing migration in Pacific salmon from behavioral to molecular biological approaches. *Gen. Comp. Endocrinol.* **170**, 222-232. doi:10.1016/j.ygcen.2010.02.003