Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon

Authors: Nathan F. Putman[1*], Kenneth J. Lohmann[2], Emily M. Putman,

Thomas P. Quinn[3], A. Peter Klimley[4], & David L.G. Noakes[1,5]

Affiliations:

1. Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

2. Department of Biology, CB #3280, University of North Carolina, Chapel Hill, NC 27599, USA

3. School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington, 98195, USA

4. Department of Wildlife, Fisheries, and Conservation Biology, University of California, Davis, One Shields Ave., Davis, CA 95616, USA

5. Oregon Hatchery Research Center, 2418 Fall Creek Road, Alsea, Oregon, 97324, USA

* author for correspondence, nathan.putman@gmail.com

Running head: Geomagnetic imprinting in Pacific salmon

Key words: navigation; orientation; magnetic map; magnetoreception; salmon; imprinting; geomagnetic secular variation

Highlights:

- Sockeye salmon use geomagnetic imprinting as a homing mechanism.
- The homing route of salmon is predicted by magnetic field drift (secular variation).

Summary:

In the final phase of their spawning migration, Pacific salmon use chemical cues to identify their home river, but how they navigate from the open ocean to the correct coastal area has remained enigmatic [1]. To test the hypothesis that salmon imprint on the magnetic field that exists where they first enter the sea and later seek the same field upon return [2-4], we analyzed a 56-year fisheries dataset on Fraser River sockeye salmon, which must detour around Vancouver Island to approach the river through either a north or south passageway [5,6]. We found that the proportion of salmon using each route was predicted by geomagnetic field drift; the more the field at a passage entrance diverged from the field at the river mouth, the fewer fish used the passage. We also found that more fish used the northern passage in years with warmer sea surface temperature (presumably because fish were constrained to more northern latitudes). Field drift accounted for 16% of the variation in migratory route used, temperature 22%, and the interaction among these variables 28%. These results provide the first empirical evidence of geomagnetic imprinting in any species and imply that forecasting salmon movements is possible using geomagnetic models.

Results:

Natal homing, a pattern of behavior in which animals return to reproduce in the same geographic area where they originated, occurs in diverse animals, including some that migrate thousands of kilometers between foraging and breeding sites. The navigational mechanisms that underlie natal homing are not well understood for any species [*7-10*]. Marine animals such as sea turtles, seals, and anadromous fishes have been hypothesized to "imprint" on the magnetic fields associated with their coastal reproductive areas and to use that information to return months or years later [*2-4*]. Because Earth's magnetic field varies predictably across the globe, animals might use magnetic parameters as a "map" to determine their geographic location [*4, 10*]. Experiments have revealed that oriented swimming responses can be elicited by magnetic field information in diverse marine migrants [*11-13*]. However, no further evidence either supporting or refuting the magnetic imprinting hypothesis has been obtained.

We used a novel approach for testing the magnetic imprinting hypothesis by examining fisheries data on sockeye salmon (*Oncorhynchus nerka*), a commercially important fish [*14*] that is well-known for its homing [*1*] and capable of orientation to Earth-strength magnetic fields [*11, 15*]. Sockeye salmon from the Fraser River typically spend 2 years at sea, distributed widely throughout the Gulf of Alaska, prior to the onset of their homeward migration [*16, 17*]. Their return to the Fraser River is blocked by Vancouver Island and the fish must either follow a southerly route through the Strait of Juan de Fuca or a northerly route through Queen Charlotte Strait to reach the river mouth (Fig. 1a). The geographical constraint imposed by Vancouver Island on the sockeye spawning migration to the Fraser River, combined with 56 years of fisheries data on the proportion of fish using the northern route (i.e., the "diversion rate") [*5, 6*], provides a unique opportunity to test the magnetic imprinting hypothesis of natal homing (Fig. 1a). If salmon imprint on the magnetic field when they make the transition to seawater [*2, 4*], then whether fish return by the northern or southern route might be influenced by subtle changes in the field near Vancouver Island. Specifically, their return route might reflect how closely the field at each entryway, at the time when the fish return, resembles the field that fish experienced 2 years previously as they left the Fraser River. We reasoned that, all else being equal, a greater proportion of fish should use the northern entryway when the difference between the magnetic fields at Queen Charlotte Strait and the Fraser River is small; thus, as the difference in fields between these two locations increases, the diversion rate should decrease. By contrast, when the difference between the magnetic field at the Strait of Juan de Fuca and the Fraser River is small, a greater proportion of fish should take the southern route, and as the difference in fields between these two locations increases, the diversion rate should increase. We also explored the correlation between the diversion rate and other environmental factors that have been proposed to influence the diversion rate: sea surface temperature (SST) [*5, 17*], the volume of Fraser River discharge [*17*], and the velocity of ocean currents in the Gulf of Alaska [*18*] (Supplemental Table 1).

Consistent with the predictions of the magnetic imprinting hypothesis, we found that as the difference in magnetic intensity (total field strength) between the Fraser River and Queen Charlotte Strait decreased, a higher proportion of sockeye salmon migrated through the northern route (Spearman $r = -0.58$, $p = 3.2 \times 10^{-6}$) (Fig. 1b). Likewise, when the difference in magnetic intensity between the Fraser River and the Strait of Juan de Fuca decreased, a higher proportion of salmon migrated through the southern route (Spearman $r = 0.64$, $p = 1.0 \times 10^{-7}$) (Fig. 1c). Although the difference in magnetic inclination angle (the angle that field lines intersect the surface of the earth) at Queen Charlotte Strait and the Fraser River was correlated with the diversion rate the difference in inclination angle at the Strait of Juan de Fuca and the Fraser River was not (Supplemental Table 1). Moreover, upon closer examination of the inclination angle we determined that its minimal changes in magnitude (Fig. 2) were not consistent with the extraordinary fluctuations in the diversion rate (range, 2% - 85%).

Of the non-magnetic environmental factors we examined, only SST was correlated with the diversion rate (Supplemental Table 1). As was shown previously [*1, 5, 17*], in years with warmer SST a higher proportion of salmon migrated through the northern route (Spearman $r = 0.69$, $p = 5.5 \times 10^{-9}$) (Fig. 1d). For further analysis, we focused our attention on the change in magnetic intensity at the northern and southern entryways and SST. Multiple regression analyses revealed that 66% of the variation in diversion rate could be accounted for by the combination of differences in magnetic intensity and SST (Table 1). Variance partitioning indicated that 16% of the variation in diversion rate could be uniquely ascribed to the differences in magnetic intensity at the two entryways relative to the Fraser River, 22% of the variation could be attributed to SST, and the remaining 28% is ascribed to the combination of these factors.

Discussion

These results provide the first empirical support for the magnetic imprinting hypothesis of natal homing and imply that sockeye salmon use geomagnetic cues to guide the open-sea portion of their spawning migration. Although exactly how salmon determine their location at sea relative to their natal river is not known, doing so likely enhances the benefits of their anadromous life-history. Efficiently navigating from oceanic foraging grounds to the correct coastal location maximizes time available for feeding, minimizes loss of energy stores in transit, and ensures the fish reach spawning sites at the appropriate time [*1, 2*]. We speculate that sockeye salmon (and presumably other salmon species [*1*]) might assess location using a "map sense" based in part on magnetic intensity and inclination angle [*13*]. The mouth of the Fraser River is unambiguously defined by the combination of magnetic intensity and inclination angle (Fig. 2), as are most other locations along the Pacific coast of North America where salmon exist. In the Gulf of Alaska these magnetic parameters could be used to effectively return to the vicinity of the coastal imprinting site using any one of several strategies that function with a non-orthogonal, bicoordinate grid [*2, 10, 19, 20*] (Fig. S1); thereafter olfaction is used to complete the freshwater phase of the migration [*1, 4*].

A complication, however, for many of the proposed open-sea navigational strategies is that fish can become "trapped" in coastal areas as a result of slight navigational errors or beginning the migration close to coastlines [*1, 21*]. For much of the past century the magnetic intensity gradient ran parallel to the British Colombia coastline (Figs. 2a-2c), thus a simple solution would have been for salmon to follow the isoline of magnetic intensity associated with the mouth of the Fraser River southwards had they encountered it [*4*]. Following this isoline would have reliably led salmon to the Fraser River via Queen Charlotte Strait (Fig. 2). The Fraser River isoline of intensity has gradually drifted westward into the Gulf of Alaska and the proportion of sockeye salmon that encounter the isoline has likely increased with time (Fig. 2); presumably increasing the percentage of salmon that migrate through the northern route. Such an effect would be magnified in warmer years when sockeye salmon have a more northerly distribution [*5 ,17, 22*], further increasing the proportion of the population that encounters the isoline of magnetic intensity associated with the home river (Fig. 3).

This interactive influence of magnetic field drift and SST on diversion rate (Table 1) may explain some of the apparent outliers in the relationship between diversion rate and magnetic field drift. For instance, in 2008 total field intensity at Queen Charlotte Strait was only 138 nT different from the Fraser River mouth in 2006 (the lowest in the 56 year dataset), though only 10% of fish used this route. However, 2008 had the third coldest SST for the 56 year dataset, which would increase the proportion of salmon beginning their migration from more southerly latitudes and likewise the proportion of salmon migrating through the southerly route (Fig. 3). On a longer timescale, the gradual change in alignment of the magnetic intensity gradient across the North Pacific may explain why few sockeye salmon used the northern migratory route in the early part of the century [*5*], even though the range of SST was comparable to more recent times (1935-1953 SST range = 7.4-10.9°C; 1953-2012 SST range = 7.6-10.5°C). Prior to the 1970s the magnetic intensity associated with the Fraser River did not extend into the Gulf of Alaska and fish would have been less likely to be led into the Queen Charlotte Strait by this cue (Figs. 2A-2B). We therefore hypothesize that the alignment of the magnetic intensity gradient is responsible for the larger decadal trends observed in the diversion rate whereas SST controls year-to-year variability.

Regardless of the organization of salmon's "magnetic map" and its interaction with other environmental factors, our analyses suggest that Earth's magnetic field plays an important role in the oceanic movements of sockeye salmon and that variability in their migratory routes is influenced by geomagnetic secular variation. These findings call for experiments on the navigational abilities of adult salmon as well as further investigation into the magnetic imprinting hypothesis of natal homing in other species such as sea turtles, migratory birds, and marine mammals.

Procedures

The proportion of sockeye using the northerly route has been estimated by the International Pacific Salmon Fishery Commission [*5*] and, afterwards, by the Pacific Salmon Commission [*6*]. In sum, these commissions generated continuous annual estimates for the years 1953-2008. Before the late 1970s nearly all fish traveled via the southerly route, through the Strait of Juan de Fuca, to reach the Fraser River (Fig. S2). Thus, the percentage of fish travelling via the northern route was known as the "diversion rate." Fish following the northerly route travel exclusively through Canadian waters (and fisheries) whereas those following the southerly route travel through an area shared by Canadian and the United States fisheries [5, *6*]. Predicting the proportion of fish following each route has received considerable attention from researchers due to important economic and management implications [*1, 17, 18, 21-27*].

To examine geomagnetic secular variation in the vicinity of the Fraser River we used the International Geomagnetic Reference Field model (IGRF-11) [*28*]. We determined the values of both magnetic field strength (total field intensity) and inclination angle (the angle that field lines intersect Earth's surface) at the mouth of the Fraser River (49.1° N, 123.25° W), the seaward entry to Queen Charlotte Strait (51.0° N, 128.0° W), and the seaward entry to the Strait of Juan de Fuca (48.45° N, 124.6° W). Sensitivity to these magnetic parameters is known in sea turtles [*13*] and appears likely in the rainbow trout (*O. mykiss*) [*29, 30*], a species that is congeneric with sockeye salmon. We calculated the difference in magnetic values between the mouth of Fraser River and each entryway assuming a 2 year time lag between fish leaving the river as juveniles (April-May) and returning to spawn at maturity (June-August) [*17*].

When examining additional environmental factors, we attempted to make our analyses comparable to those performed previously and thus used the same data sources and seasonal periods as earlier studies on Fraser River sockeye salmon [*5, 17, 18*]. April SST data were from the Kains Island Lighthouse (50.27° N, 128.02° W), provided by Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm). Data on Fraser River discharge between April and June were taken at a station near Hope, British Columbia, provided by the Water Survey of Canada (http://www.wsc.ec.gc.ca/staflo/index_e.cfm?cname=HydromatD.cfm). Ocean surface currents were modeled with the Ocean Surface Current Simulator (OSCURS) and the northward advection of virtual particles was calculated between May 1 and June 30 at 3 locations in the Gulf of Alaska: (1) 50° N, 150° W; (2) 50° N 140° W; and (3) 50° N 130° W (http://las.pfeg.noaa.gov/oscurs/). Spearman's Correlation Test (non-parametric) was used to examine the relationship between each variable and the diversion rate from 1967-2008. This range of dates was chosen because ocean currents modeled by OSCURS were available starting in 1967. After determining the variables of interest (magnetic intensity and SST) we performed Spearman's Correlation Test, linear regressions, and variance partitioning analyses with these variables for the full dataset on the diversion rate (1953-2008).

Acknowledgements:

N.F.P. designed the research and performed analyses, all authors contributed to interpretation of the data, N.F.P. wrote the paper with input from all authors. Financial support was provided by Oregon Sea Grant, the Oregon Department of Fish and Wildlife, Oregon State University to D.L.G.N. and National Science Foundation grant IOS-1022005 to K.J.L.

References:

1. Quinn, T.P. (2005). *The Behavior and Ecology of Pacific Salmon and Trout*, University of Washington Press, Seattle.

2. Quinn, T.P. (1982) A model for salmon navigation on the high seas. In: E.L. Brannon and E.O. Salo (editors), *Salmon and Trout Migratory Behavior Symposium*. School of Fisheries, University of Washington, pp. 229-237.

3. Putman, N.F., and Lohmann, K.J. (2008). Compatibility of magnetic imprinting and secular variation. Current Biology *18*, R596-R597.

4. Lohmann, K.J., Putman, N.F., and Lohmann, C.M.F. (2008). Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proceedings of the National Academy of Sciences USA*, **105**, 19096-19101.

5. International Pacific Salmon Fisheries Commission (IPSFC), (1954-1986). *Annual Report 1953-1985*, (New Westminster, Canada: Int. Pac. Salmon Fish. Comm.).

6. Pacific Salmon Commission (1988-2012). *Report of the Fraser River panel to the Pacific Salmon Commission on the 1986-2008 Fraser River Sockeye Salmon Fishing Season*, (Vancouver, B.C.: Pacific Salmon Commission).

7. Alerstam, T. (2006). Conflicting evidence about long-distance animal navigation. Science, *313*, 791-794.

8. Lohmann, K.J. (2010). Magnetic-field perception: News and Views Q&A. Nature, *464*,1140-1142.

9. Lohmann, K.J., Lohmann, C.M.F., and Endres, C.S. (2008) The sensory ecology of ocean navigation. Journal of Experimental Biology, *211*, 1719-1728.

10. Lohmann, K.J., Lohmann, C.M.F., and Putman, N.F. (2007). Magnetic maps in animals: nature's GPS. Journal of Experimental Biology *210*, 3697-3705.

11. Quinn, T.P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. Journal of Comparative Physiology *137*, 243-248.

12. Walker, M.M. (1984). Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. Journal of Comparative Physiology - A *155*, 673-679.

13. Putman, N.F., Endres, C.S., and Lohmann, C.M.F., and Lohmann, K.J. (2011) Longitude perception and bicoordinate magnetic maps in sea turtles. Current Biology *21*, 463-466.

14. Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V. , and Kurashov, V. (1999). The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. *56*, 516-526.

15. Quinn, T.P. and Brannon, E.L. (1982). The use of celestial and magnetic cues by orienting sockeye salmon smolts. Journal of Comparative Physiology *147*, 547-552.

16. Burgner, R.L. (1991) Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-117 *in* C. Groot, and L. Margolis, editors. *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver.

17. Groot, C. and Quinn, T.P. (1987). Homing migration of sockeye salmon, *Oncorhynchus nerka*, to the Fraser River. Fishery Bulletin *85*, 455-469.

18. Thomson, K.A., Ingraham, W.J., Healey, M.C., Leblond, P.H., Groot, C., and Healey, C.G. (1992). The influence of ocean currents on latitudinal landfall and migration speed of sockeye salmon returning to the Fraser River. Fisheries Oceanography *1*, 163-179.

19. Gould, J.L. (1998) Sensory bases of navigation. Current Biology *8*, R731-R738.

20. Benhamou, S. (2003). Bicoordinate navigation based on non-orthogonal gradient fields. Journal of Theoretical Biology *225*, 253-239.

21. Pascual, M.A. and Quinn, T.P. (1991). Evaluation of alternative models of the coastal migration of adult Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. *48*, 799-810.

22. Blackbourn, D.J. (1987). Sea surface temperature and pre-season prediction of return timing in Fraser River sockeye salmon (*Oncorhynchus nerka*). Canadian Special Publication of Fisheries and Aquatic Sciences *96*, 296-306.

23. Gilhousen, P. (1960). Migratory behavior of adult Fraser River sockeye. International Pacific Salmon Fisheries Commission Progress Report *7*, 78 p.

24. Hamilton, K. (1985). A study of the variability of the return migration route of Fraser River sockeye salmon *(Oncorhynchus nerka)*. Canadian Journal of Zoology *63*, 1930-1943.

25. Groot, C. and Cooke, K. (1987). Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? Canadian Special Publication of Fisheries and Aquatic Sciences *96*, 53-60.

26. Hsieh, W.W., Lee, W.G., Mysak, and L.A. (1991). Using a numerical model of northeast Pacific Ocean to study the interannual variability of the Fraser River sockeye salmon (*Oncorhynchus nerka)*. Canadian Journal of Fisheries and Aquatic Sciences *48*, 623-630.

27. Hodgson, S., Quinn, T.P., Hilborn, R., Francis, R.C., Rogers, D.E. (2006). Marine and freshwater climatic factors affecting interannual variation in the timing of return migration to fresh water of sockeye salmon (*Oncorhynchus nerka*). Fisheries Oceanography *15*, 1-24.

28. Finlay, C.C. et al. (2010). International Geomagnetic Reference Field: the eleventh generation. Geophysical Journal International *183*,1216-1230.

29. Hellinger, J., Hoffman, K.P. (2009). Magnetic field perception in the Rainbow Trout, *Oncorhynchus mykiss*. J. Comp. Physiol. A *195*, 873-879.

30. Eder, S.H.K., Caidou, H., Muhamad, A., McNaughton, P.A., Kirschvink, J.L., and Winklhofer, M. (2012). Magnetic characterization of isolated candidate vertebrate magnetoreceptor cells. Proceedings of the National Academy of Sciences USA*109*, 12022-12027.

Figure Legends

Figure 1. (A) Map of the study area. Fish attempting to return to the Fraser River must travel around Vancouver Island via Queen Charlotte Strait or the Strait of Juan de Fuca. Scale bar length is 225 km. (B) Relationship between the diversion rate (the percentage of fish following the northern migratory route through Queen Charlotte Strait) and the difference in magnetic intensity between the mouth of the Fraser River and Queen Charlotte Strait. (C) Relationship between the diversion rate and the difference in magnetic intensity between the mouth of the Fraser River and the Strait of Juan de Fuca. (D) Relationship between the diversion rate and April SST at Kains Island lighthouse on northwest Vancouver Island. Trend lines are estimated by linear regression.

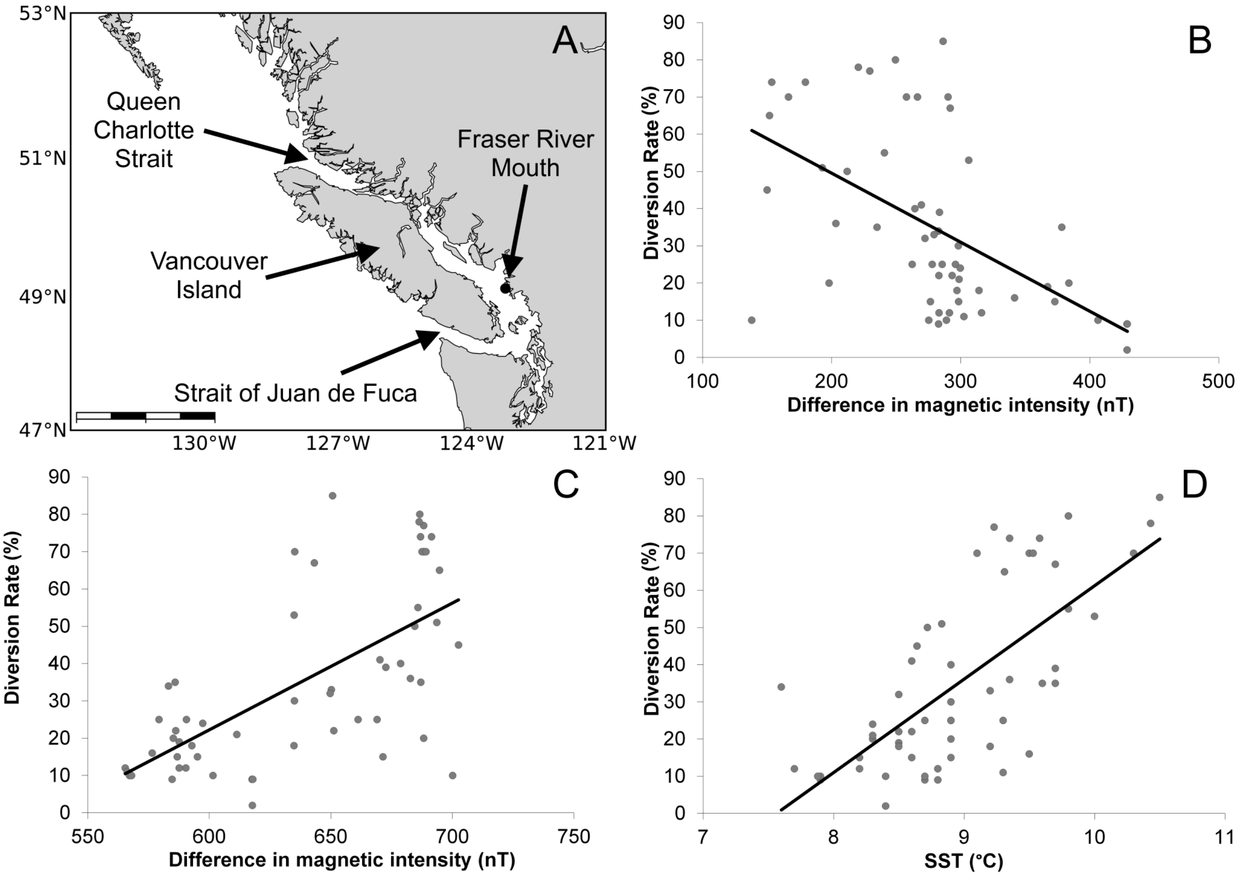


Figure 2 Maps of the Northeast Pacific showing the isolines of magnetic intensity (red) and inclination angle (blue) that exist at the mouth of the Fraser River (white circle). Inset figures show magnetic parameters in the immediate vicinity of Vancouver Island (scale bar length is 225 km). Isolines are based on the IGRF-11 [*28*] and assume that fish resolve intensity at ±250 nT and inclination angle at ± 0.25°. Although the resolution with which salmon detect these magnetic parameters is unknown, the values shown here would average out most magnetic noise from diurnal variation, ocean currents, and anomalies from the Earth's crust. Magnetic values are plotted assuming a 2 year ocean-stage for sockeye salmon, in which fish do not compensate for secular variation (field drift), but rely on the same magnetic values they remember from their initial seaward migration. The locations of magnetic values that existed at the Fraser River in (A) 1900 plotted two years later, in 1902; (B) 1951 plotted in 1953; (C) 1976 plotted in 1978; and (D) 2008 plotted in 2010. Relatively few sockeye salmon used the northern route through the Queen Charlotte Strait to reach the Fraser River prior to the 1970's. However, this route has become increasingly common as the magnetic intensity isoline has drifted further into the Gulf of Alaska.

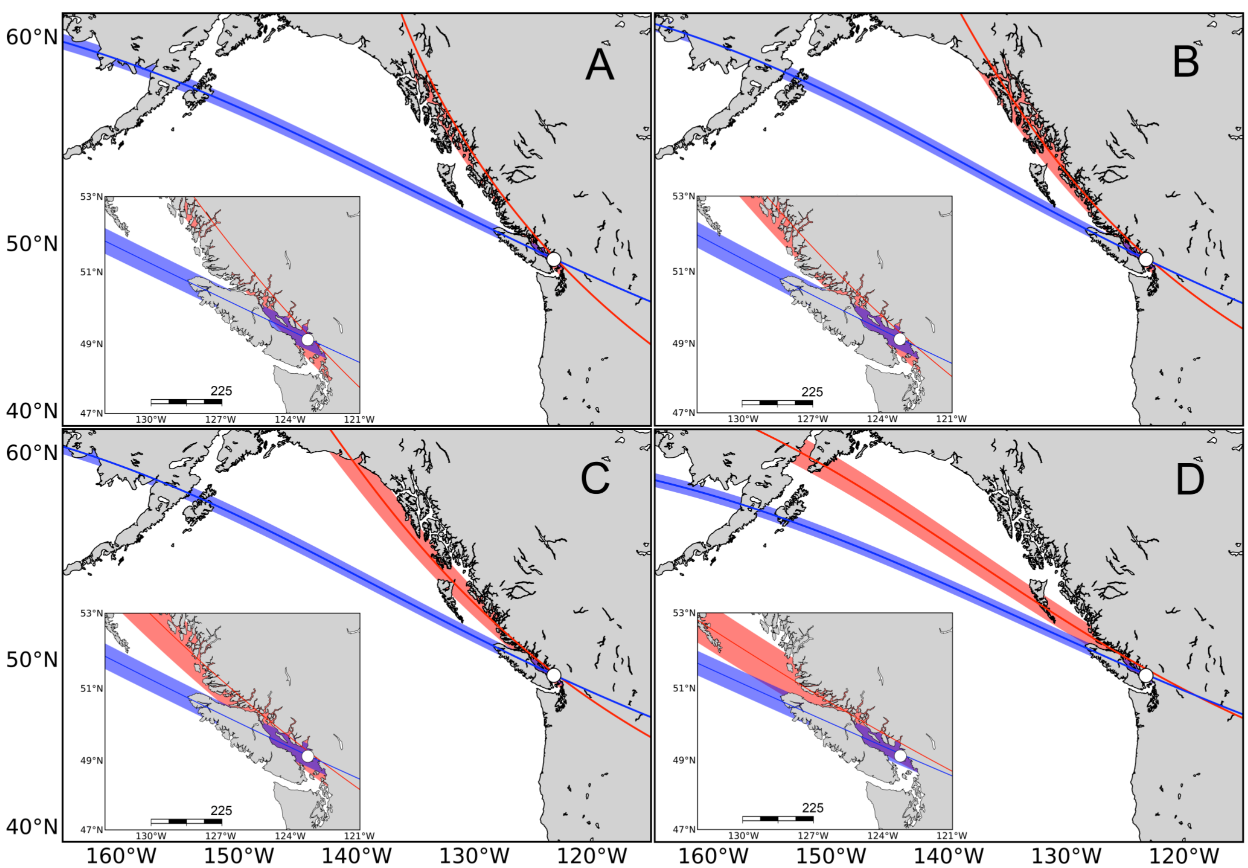
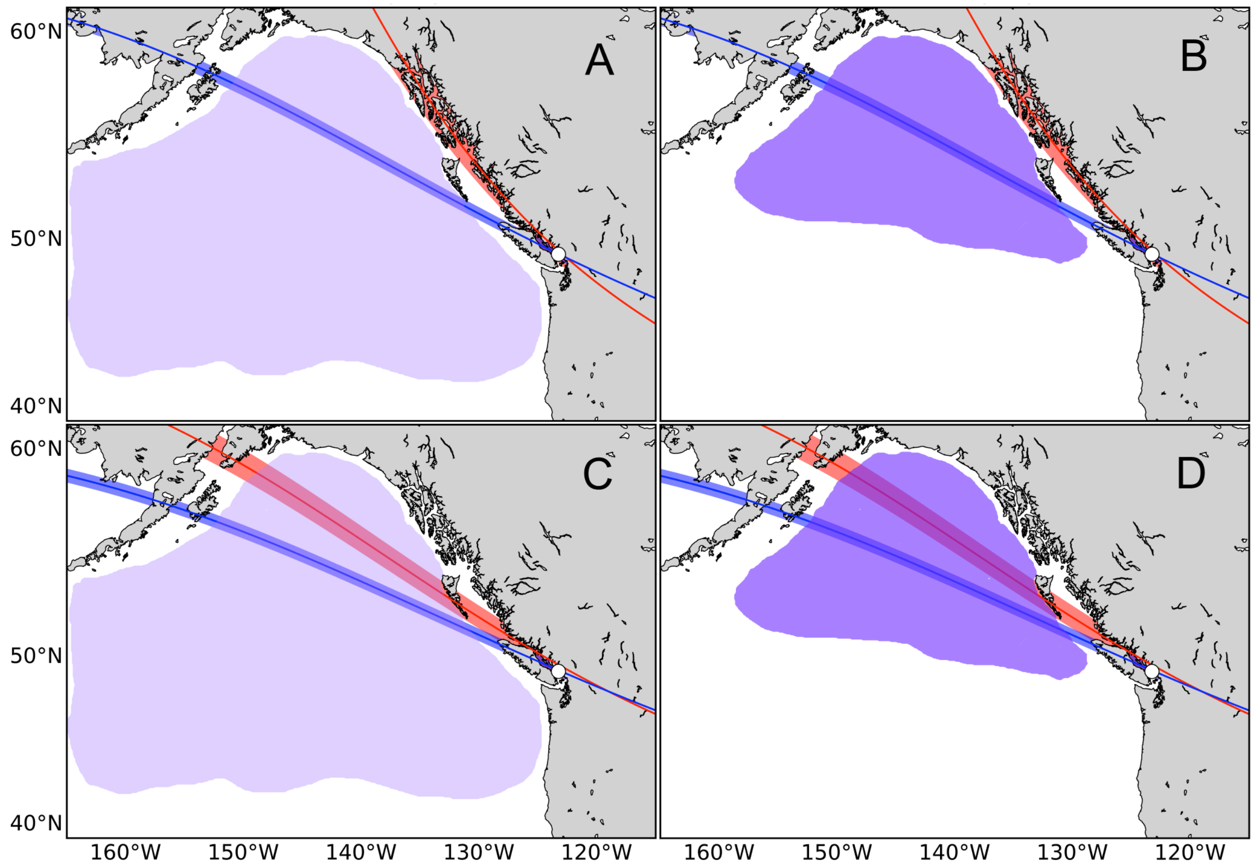


Figure 3. Hypothetical interaction between salmon distribution and sea surface temperature (SST) influencing the proportion of the population that encounters the magnetic intensity isoline associated with the Fraser River while in the Gulf of Alaska. Purple indicates the hypothetical distribution of salmon in the North Pacific (darker shading implies greater density). Red and blue lines indicate magnetic intensity and inclination angle, respectively. The magnetic data plotted are from 1953 (A, B) and 2010 (C, D). A bicoordinate navigational strategy is likely more efficient for migrating from the open sea to the Fraser River than using a single coordinate of the magnetic field (e.g., Supplemental Fig 1). However, fish that encounter the magnetic intensity isoline associated with the Fraser River could take a relatively direct route homeward by swimming along that isoline (and into Queen Charlotte Strait). Thus, we propose that sockeye salmon use bicoordinate navigation for homing except when the fish encounter the magnetic intensity associated with the Fraser River, which elicits them to swim along the isoline. Such a homing strategy would result in major differences in diversion rate among years and be greatly influenced by the starting locations of fish and thus SST. In years when SST is cool, sockeye salmon are likely to be distributed widely throughout the North Pacific (A, C). Thus in cool years, the proportion of fish that encounter the isoline of magnetic intensity associated with the Fraser River is relatively low, regardless as to whether the isoline is near the coast or farther west. However, when SST is warm, sockeye are likely to be constrained to more northern latitudes (B, D), thus increasing the proportion of the population that encounters the isoline of magnetic intensity associated with the Fraser River. Based on the interaction between SST and magnetic intensity we would expect diversion rate would be low in (A), moderate in (B), moderate in (C), and high in (D).



A
B
C
D
60°N
50°N
40°N
160°W
150°W
140°W
130°W
120°W

Table Legends

Table 1. Results of regression analyses predicting the annual diversion rate (1953-2008) (see Supplemental Figure 2). Diversion rate (d) is predicted as a function of the difference in magnetic intensity between the Fraser River and Queen Charlotte Strait (q), the difference in magnetic intensity between the Fraser River and Strait of Juan de Fuca (j), and the mean April SST at Kains Island Lighthouse on Vancouver Island (t). Other abbreviations follow conventions in Table 1.

Predictors	**R^2 (p)**	**Equation**
Δ Intensity QCS	0.29 (<0.0001)	d = -0.185q +87
Δ Intensity JDF	0.43 (<0.000001)	d = 0.34j -181
SST	0.50 (<0.000001)	d = 25.2t – 190
Δ Intensity QCS + Δ Intensity JDF + SST	0.66 (<0.00000001)	d = 18.6t - 0.067q +0.148j - 207

Supplemental Material:

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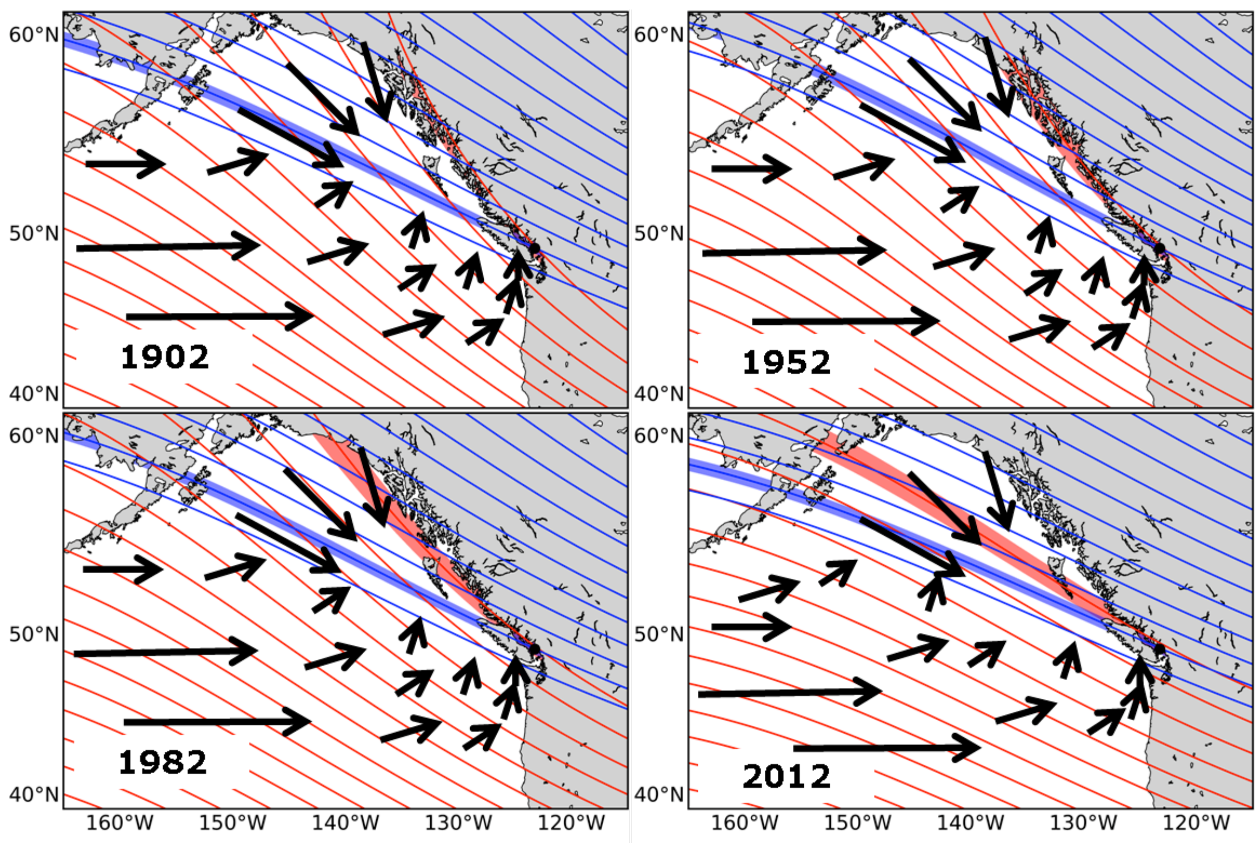
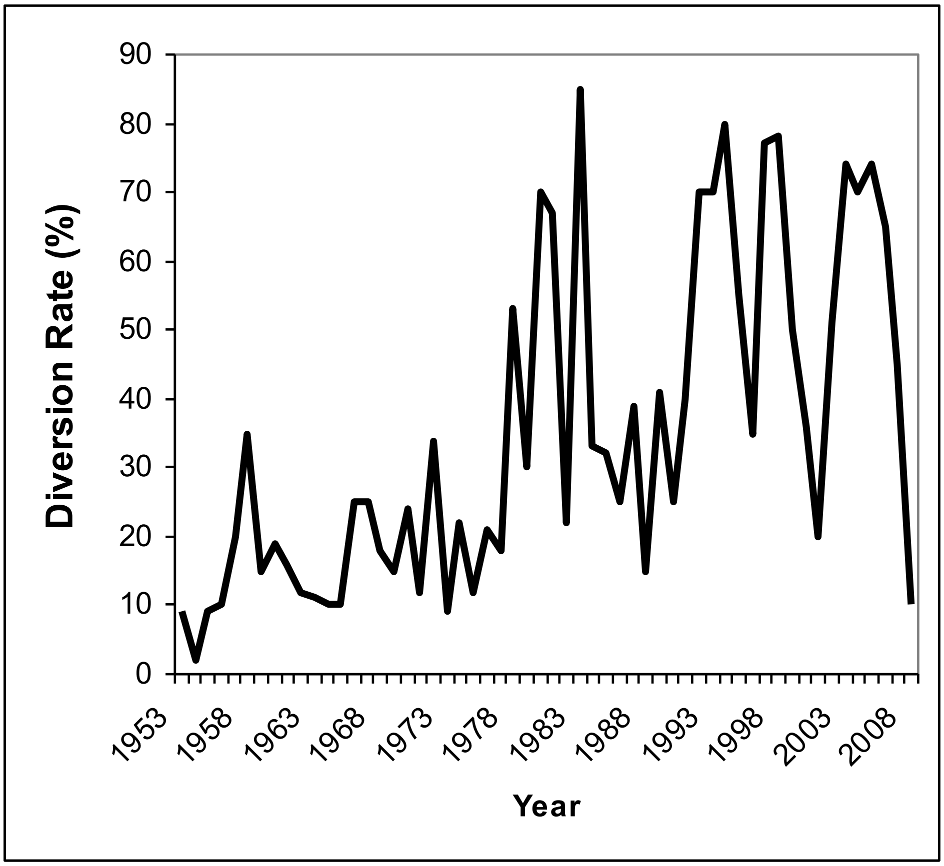
Supplemental Figures

Supplemental Figure 1. Hypothetical navigational strategy based on gradients of magnetic intensity and inclination angle. Sockeye salmon swim southeastwards when in magnetic fields with steep inclination angles (relative to the imprinted value), increasingly orienting eastward as inclination angle decreases. At inclination angles less steep than a threshold value (~1° less than the imprinted value) fish assess location based on intensity. Fish orient northeastward, with an increasing northward component as intensity becomes closer to the imprinted value. In these diagrams the gradients of inclination angle (blue) and intensity gradient (red) are plotted over the areas in which sockeye salmon would use them to orient their movement homeward. Thicker lines of each color are the value associated with the mouth of the Fraser River. Black arrows indicate the direction that salmon would adopt based on the magnetic cues encountered at a given location. This strategy would allow for efficient transit from the open sea to vicinity of the Fraser River for the past century.



Supplemental Figure 2. Time series of diversion rate.



Supplemental Table

Supplemental Table 1. Spearman's correlation between environmental factors and diversion rate (1967-2008). Factors include: (QCS) the difference in IGRF magnetic intensity and inclination angle after 2 years between Queen Charlotte Strait and the mouth of the Fraser River; (JDF) the difference in IGRF magnetic intensity and inclination angle after 2 years between the Strait of Juan de and the mouth of the Fraser River; (SST) the mean April SST at Kains Island Lighthouse; the northward advection of virtual particles released at different locations in the OSCURS model between May 1 and June 30; and the mean volume of water discharged from the Fraser River for April, May, and June.

Variable	**Spearman's r (p)**
Δ Intensity QCS	-0.41 (0.007)
Δ Inclination QCS	-0.37 (0.015)
Δ Intensity JDF	0.54 (0.0002)
Δ Inclination JDF	0.05 (0.748)
SST	0.74 (<0.0001)
Northward Current Velocity 50° N, 150° W	-0.07 (0.632)
Northward Current Velocity 50° N, 140° W	-0.13 (0.319)
Northward Current Velocity 50° N, 130° W	0.25 (0.113)
Fraser River Discharge	-0.15 (0.355)