© 2020. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2020) 223, jeb222091. doi:10.1242/jeb.222091

RESEARCH ARTICLE

Magnetoreception in fishes: the effect of magnetic pulses on orientation of juvenile Pacific salmon

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ABSTRACT

A variety of animals sense Earth's magnetic field and use it to guide movements over a wide range of spatial scales. Little is known, however, about the mechanisms that underlie magnetic field detection. Among teleost fish, growing evidence suggests that crystals of the mineral magnetite provide the physical basis of the magnetic sense. In this study, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) were exposed to a brief but strong magnetic pulse capable of altering the magnetic dipole moment of biogenic magnetite. Orientation behaviour of pulsed fish and untreated control fish was then compared in a magnetic coil system under two conditions: (1) the local magnetic field and (2) a magnetic field that exists near the southern boundary of the natural oceanic range of Chinook salmon. In the local field, no significant difference existed between the orientation of the control and pulsed groups. By contrast, orientation of the two groups was significantly different in the magnetic field from the distant site. These results demonstrate that a magnetic pulse can alter the magnetic orientation behaviour of a fish and are consistent with the hypothesis that salmon have magnetite-based magnetoreception.

KEY WORDS: Chinook salmon, Magnetoreception, Magnetic field, Magnetite, Navigation, *Oncorhynchus tshawytscha*

INTRODUCTION

Diverse animals detect Earth's magnetic field and use it as a cue to guide their movements (Wiltschko et al., 1993; Kimchi and Terkel, 2001; Boles and Lohmann, 2003; Naisbett-Jones et al., 2017; Lohmann and Lohmann, 2019). Little is known, however, about the mechanism (or mechanisms) that enable animals to sense magnetic fields. Recent research has focused on two possibilities. The chemical magnetoreception (or radical pairs) hypothesis proposes that the detection of magnetic fields involves biochemical reactions that are influenced by the ambient magnetic field (Ritz et al., 2000; Rodgers and Hore, 2009). By contrast, the magnetite hypothesis proposes that crystals of the magnetic mineral magnetite (Fe_3O_4) underlie magnetoreception (Kirschvink et al., 2001; Shaw et al., 2015). It is possible that different animals have different mechanisms, that both mechanisms coexist in some animals (Johnsen and Lohmann, 2005; Lohmann, 2010), and also that magnetoreception is accomplished by a different biophysical process (e.g. Nimpf et al., 2019).

Two main lines of evidence are consistent with the magnetite hypothesis. The first is that magnetic material has been detected in many magnetically sensitive species (Lohmann, 1984; Kirschvink et al., 1985; Moore et al., 1990; Moore and Riley, 2009). The second is that strong but brief magnetic pulses alter magnetic orientation behaviour in several animals, including lobsters (Ernst and Lohmann, 2016), turtles (Irwin and Lohmann, 2005), birds (Beason et al., 1995) and bats (Holland et al., 2008). The effect of magnetic pulses on behaviour is noteworthy because such pulses have the potential to modify the magnetic dipole moment of magnetite crystals, which in turn might alter magnetic information relayed to the brain by magnetite-based receptors (Wiltschko et al., 2002). Importantly, magnetic pulses should have no lasting effect on animals that rely on chemical magnetoreception (Shaw et al., 2015). For this reason, subjecting animals to strong magnetic pulses and monitoring subsequent changes in behaviour has often been described as a diagnostic test for magnetite-based magnetoreception (Beason et al., 1995; Wiltschko et al., 1998; Holland et al., 2008).

Fish have played a prominent role in magnetoreception research (Putman et al., 2014a; Bottesch et al., 2016; Naisbett-Jones et al., 2017) and magnetite has been detected in several species (Walker et al., 1984; Kirschvink et al., 1985; Diebel et al., 2000). However, whether a magnetic pulse affects the orientation behaviour of fish is not known. Here, we report such an experiment with Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum 1792), a migratory fish that uses Earth's magnetic field for orientation (Putman et al., 2014a, 2018) and is known to possess chains of single-domain magnetite particles that might function as magnetoreceptors (Kirschvink et al., 1985). The results indicate that a magnetic pulse alters subsequent magnetic orientation behaviour in young salmon, a finding consistent with the hypothesis that magnetoreception in salmon, and perhaps in other teleost fish, is at least partly based on magnetite.

MATERIALS AND METHODS

Animals and facilities

Chinook salmon from the Elk River, OR, USA, were spawned in December 2016 from a mix of wild and hatchery adults (29 pairs). Fertilized eggs were incubated at the Elk River hatchery (Port Orford, OR, USA; 42.73°N, 124.44°W) and transported at the eyed stage to the Oregon Hatchery Research Center (Alsea, OR, USA; 44.40°N, 123.75°W) in January 2017. After hatching, fish were transferred into plastic, circular outdoor holding tanks (0.9 m diameter). Holding tanks received a continuous supply of natural stream water. Water parameters varied with ambient conditions. Between June and July 2017, we tested a total of 432 stream-dwelling Chinook salmon parr (fork lengths ranged from 5 to 7 cm). All animal care and procedures were approved by the Institutional

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Received 23 January 2020; Accepted 4 April 2020

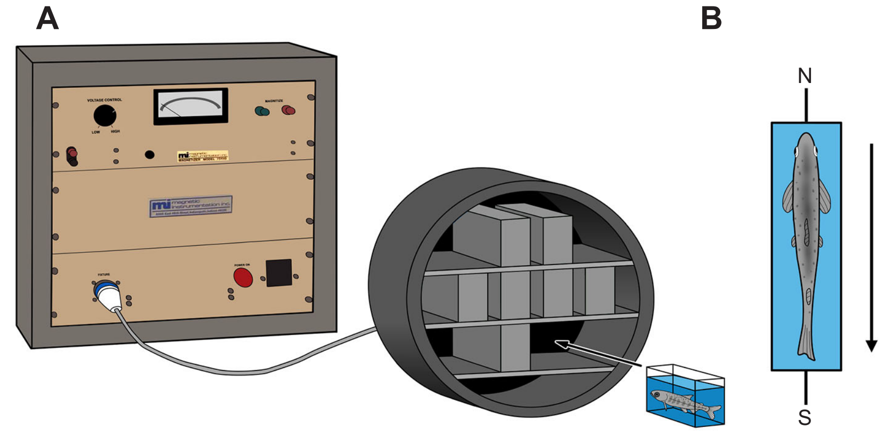

Fig. 1. Magnetic pulse procedure. (A) Magnetizer and solenoid. Diagram shows the positions of the eight pulsing chambers in which all fish were placed prior to being tested in orientation experiments. Fish in the pulse group were subjected to a magnetic pulse, control fish were not. (B) View of pulsing chamber from above. Fish were placed into the solenoid facing north. Arrow indicates the direction of the pulse with respect to ambient magnetic field conditions.

Animal Care and Use Committee of Oregon State University (approval number 4761) and the University of North Carolina (approval number 17-189).

Magnetic pulse protocol

Fish were randomly assigned to one of two treatment groups. One group of fish was treated with a strong magnetic pulse (85 mT) capable of realigning the magnetic dipole moments of single-domain biogenic magnetite crystals (Ernst and Lohmann, 2016). The second group of fish served as controls and were subjected to identical handling, but not exposed to a magnetic pulse.

The magnetic pulse was generated with a magnetizer (model 7515-G, Magnetic Instrumentation, Indianapolis, IN, USA). The magnetizer consisted of a bank of capacitors (425 V max) that discharged to a solenoid (Fig. 1A). The solenoid (32 cm diameter, 20 cm length) was aligned with the magnetic north–south axis.

During the pulsing procedure, fish were individually placed into non-magnetic pulsing chambers (6×15×2.5 cm; Fig. 1A). Each pulsing chamber was constructed of black acrylic and was filled with water to a depth of 5 cm. These chambers were designed to align fish along a single axis while preventing them from turning around. Salmon were placed into the solenoid facing north and pulsed in two groups of eight fish, one directly after the other (Fig. 1A). Pulsed fish experienced a magnetic pulse directed antiparallel to the horizontal component of the geomagnetic field (i.e. toward magnetic south) (Fig. 1B).

Testing procedure

We designed our experiment to provide two different contexts in which differential orientation might be expressed by pulsed and control salmon: (1) in the local magnetic field and (2) during a ‘magnetic displacement’ in which fish were tested in a magnetic field that exists at a distant location near the southern border of the Chinook salmon oceanic range. In a previous study (Putman et al., 2014a), this field elicited northward orientation in Chinook salmon slightly older than the ones we tested.

Our orientation assay was similar to that used by Putman et al. (2014a). Following the magnetic pulse treatment, we tested the magnetic orientation behaviour of the fish inside a magnetic coil system (Fig. 2A). Fish from the control and pulse groups were tested separately, with tests for the two groups alternated throughout the day. Prior to testing, each fish was placed into one of 16 opaque circular buckets (diameter: 30.5 cm; water depth: 20 cm) within the magnetic coil. The fish were then given a 5-min acclimation period in the local magnetic field (coil turned off), after which the orientation behaviour of fish in the same field was recorded for the next 5 min (see Fig. 3 for detailed timeline). We then used the magnetic coil to generate the magnetic field that exists in the ocean at the southern limit of the Chinook salmon’s range (Putman et al., 2014a). Salmon experienced this southern magnetic field for 10 min before the completion of the trial. Fish from both treatment groups experienced the same testing procedure within the magnetic coil. Each fish was tested only once and experienced the local ambient field before being exposed to the southern field (Fig. 3). In total, 224 fish were tested in the control treatment and 208 were tested in the pulse treatment.

Magnetic field conditions

A triaxial fluxgate magnetometer (Applied Physics model 520A) was used to measure the magnetic fields fish experienced. Within

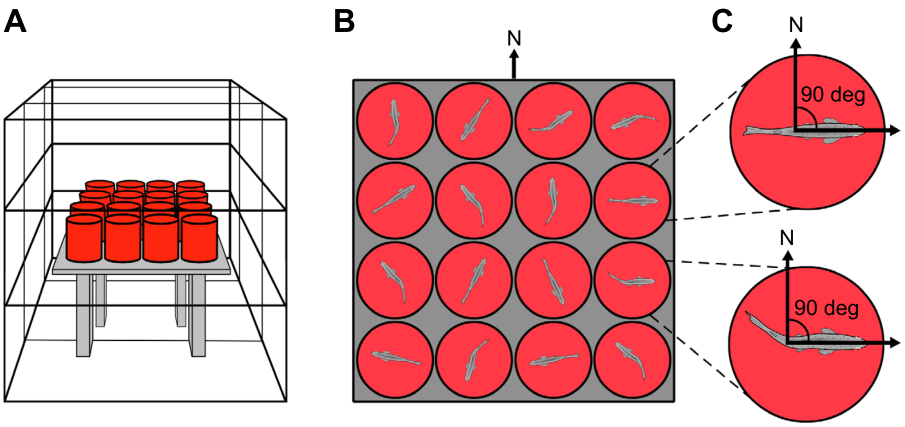

Fig. 2. Magnetic coil system and orientation arenas. (A) Schematic of the magnetic coil, table and 16 orientation arenas used in the study. The magnetic coil system consisted of two orthogonal Merritt 4-coil systems (Merritt et al., 1983). The outer, vertical coil side length was 3.32 m; the inner, horizontal coil side length was 3.05 m. Additional information about the coil is provided in Putman et al. (2014a). (B) Camera view from above the magnetic coil system showing the 16 fish in their individual arenas. (C) Examples of how fish orientation was measured. A line was drawn from the caudal peduncle to the snout to record the angle of orientation.

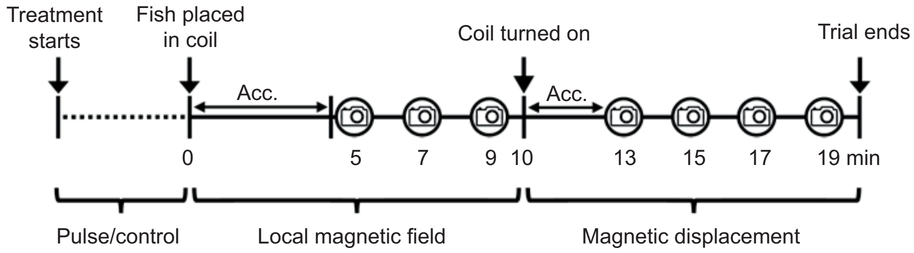

Fig. 3. Timeline of the experiment. After each group of fish was placed into the solenoid and subjected to either the pulse or control procedure (see Materials and Methods for details), fish were placed into the magnetic coil at time 0 and given a 5-min acclimation period (Acc.). Fish then experienced an additional 5 min in the local magnetic field conditions, during which several photographs (time points indicated by camera icons) were taken at 2-min intervals for the purpose of assessing orientation in this field (see Materials and Methods). The coil was then turned on and fish experienced a magnetic field that exists near the southern limit of the Chinook salmon range. After a 3-min acclimation period in the new field, several photographs were taken at 2-min intervals for the purpose of assessing orientation in the displacement field. Trials concluded after fish had been in the arena for a total of 20 min.

the holding tanks, field intensity was 51.9 µT and the inclination angle was 67.0 deg. In the magnetic coil system, the local ambient magnetic field had an intensity 51.7 µT and an inclination of 66.3 deg. The magnetic field intensity of the southern treatment field was 44.1 µT (uniformity: ±0.1 µT) and the inclination angle was 56.7 deg (uniformity: ±0.5 deg). This southern magnetic field replicated one that exists at a location (38°N, 145°W) near the southern border of the Chinook salmon range, as determined using the International Geomagnetic Reference Field (IGRF-11; Finlay et al., 2010) for June 2017, when the experiment began.

Data collection and analysis

Two GoPro cameras positioned above the coil system (Fig. 2B) were programmed to take photos at specific time points (shown in Fig. 3) during both the 5-min test period in the local ambient field and the following 10 min in the southern magnetic field. This resulted in two experimental conditions that we considered separately; in other words, we compared orientation between the control and pulsed fish in the local magnetic field and also in the southern displacement field.

Orientation angles were measured using the image processing program ImageJ (ImageJ 1.52a; https://imagej.net/ImageJ). Observers blind to which group fish belonged to analysed the photos by recording the orientation of each fish. This was achieved using the angle tool in ImageJ to draw a line along the body axis of each fish, from the caudal peduncle to the snout (Fig. 2C). The orientation angle relative to magnetic north was then recorded.

Using the orientation angles extracted from the photographs taken in the local field and in the southern (displacement) field (Fig. 3), we used standard procedures in circular statistics (Batschelet, 1981) to calculate a mean angle representing the orientation of each fish in each of the two fields. Because 16 fish were tested in the coil at a single time, we then calculated a single mean angle for each trial, which represented the average direction of all the fish that were tested simultaneously. This step was taken to account for the possibility that fish tested in the same trial might not have been fully independent, inasmuch as ambient conditions (e.g. lighting, cloud cover, etc.) at the time of testing might have influenced the fish in a similar way. This conservative analysis, which treated trials rather than individual fish as independent data points, resulted in a sample size of 14 for the control treatment group and 13 for the pulse group. To further explore the data, a second analysis treating each fish as an independent data point was also undertaken (Fig. S1). The two analyses yielded qualitatively identical results (see Fig. 4 and Fig. S1).

Rayleigh tests were used to determine whether each treatment group was significantly oriented. The nonparametric Mardia–Watson–Wheeler test was used to determine whether pulsed and control groups differed in their orientation under each of the two magnetic field conditions. We used the statistical software R (Version 1.1.423, https://www.r-project.org/) for analyses and to generate graphics.

RESULTS

Under local magnetic field conditions, fish from the control treatment group were significantly oriented with a mean angle of 338 deg (Rayleigh test, n=14, r=0.55, Z=4.17, P=0.01; Fig. 4A). In contrast, fish from the pulse group exhibited orientation that was statistically indistinguishable from random (Rayleigh test, n=13, r=0.37, Z=1.73, P=0.18; Fig. 4B). No significant difference between the orientation of the control and pulse groups was observed (Mardia–Watson–Wheeler test, W=2.69, P=0.26; Fig. 4A,B).

When exposed to a magnetic field that exists near the southern limit of the Chinook salmon range, control fish had orientation that was statistically indistinguishable from random (Rayleigh test, n=14, r=0.13, Z=0.22, P=0.81; Fig. 4C). In contrast, pulsed fish were significantly oriented towards the east–northeast with a mean angle of 72 deg (Rayleigh test, n=13, r=0.51, Z=3.37, P=0.03; Fig. 4D). The orientation of control and pulsed fish differed significantly (Mardia–Watson–Wheeler test, W=7.12, P=0.03; Fig. 4C,D).

DISCUSSION

The results demonstrate that a strong magnetic pulse influences the subsequent orientation behaviour of juvenile Chinook salmon. Salmon from the pulse and control groups exhibited significantly different orientation when tested in a magnetic field that exists near the southern boundary of their oceanic range (Fig. 4C,D). To our knowledge, these results are the first to demonstrate that a magnetic pulse affects orientation behaviour in fish. The findings are consistent with the magnetite hypothesis of magnetoreception, inasmuch as a magnetic pulse can potentially alter magnetite-based receptors, but should not exert any lasting effect on either chemical magnetoreception or electromagnetic induction (Wiltschko et al., 2002; Shaw et al., 2015).

Magnetic pulses have previously been demonstrated to affect magnetic orientation behaviour in a variety of terrestrial and aquatic animals, including rodents (Marhold et al., 1997a,b), bats (Holland et al., 2008), birds (Beason et al., 1995; Wiltschko et al., 1998; Holland and Helm, 2013), sea turtles (Irwin and Lohmann, 2005) and lobsters (Ernst and Lohmann, 2016). Interestingly, the effects of pulses on different species have been highly variable. In some cases, magnetic pulses led to increased dispersion in orientation bearings (Irwin and Lohmann, 2005). In others, the direction of orientation

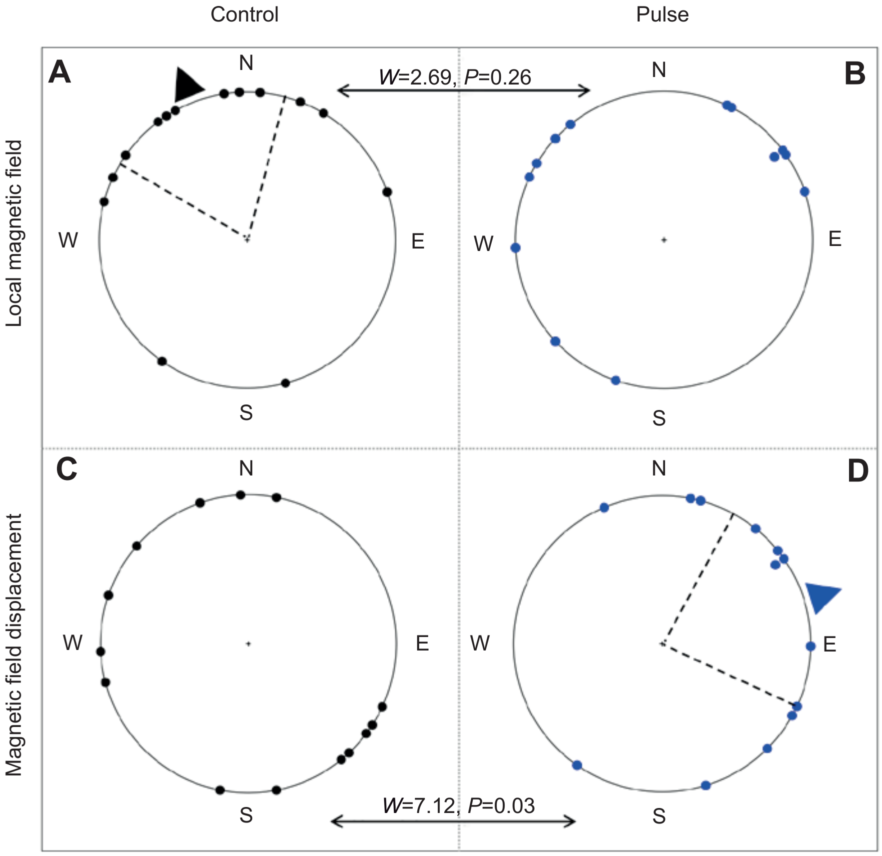

Fig. 4. Orientation of salmon under two different magnetic fields. (A) In the local magnetic field, fish from the control group were significantly oriented with a mean angle of 338 deg (Rayleigh test, *n*=14, *r*=0.55, *P*=0.01). (B) In the local magnetic field, salmon that experienced a strong magnetic pulse were not oriented as a group (Rayleigh test, *n*=13, *r*=0.37, *P*=0.18). (C) During a magnetic displacement to a southern ocean region, control fish were not oriented as a group (Rayleigh test, *n*=14, *r*=0.13, *P*=0.81). (D) During the magnetic displacement, salmon from the pulse group were significantly oriented with a mean angle of 72 deg (Rayleigh test, *n*=13, *r*=0.51, *P*=0.03). Each data point represents the mean angle of 16 fish that were tested in the coil simultaneously (see Materials and Methods). Arrowheads indicate the mean direction of each treatment group. Dashed lines represent the 95% confidence intervals for the mean.

changed after a pulse (Holland et al., 2008) or the pulse elicited a directional preference in animals that previously lacked one (Ernst and Lohmann, 2016). The variability in responses may be due in part to methodological differences such as the strength and direction of the applied pulse, the recovery period after the pulse, and the way in which animals were handled. In addition, the outcome may be influenced by the navigational task that confronts the animal during the test conditions – for example, whether it is tested in a setting that encourages homing (Beason et al., 1997; Holland et al., 2008), migration (Wiltschko and Wiltschko, 1995a) or neither (Ernst and Lohmann, 2016). Regardless, a change in orientation behaviour following treatment with a magnetic pulse has been interpreted as evidence for magnetite-based magnetoreception (Beason et al., 1995; Holland et al., 2008), although the possibility of a more general effect on the health or physiology of animals cannot be excluded with certainty (Ernst and Lohmann, 2016; Fitak et al., 2017).

Effect on magnetic compass or magnetic map?

In the present study, salmon subjected to a pulse did not differ in orientation from control fish when tested in the local magnetic field, but did differ significantly when tested in the magnetic field of a location near the southern periphery of their range (Fig. 4C,D). Interestingly, salmon are known to possess both a magnetic ‘compass’ that enables them to use Earth’s magnetic field as a directional cue (Quinn, 1980) and a magnetic ‘map’ that allows them, in effect, to assess their position within an ocean basin (Putman et al., 2014a, 2020; Putman, 2015; Scanlan et al., 2018). In principle, the mechanism underlying the compass, the map or both might have been affected by the magnetic pulse.

The salmon magnetic compass detects the polarity of the ambient field (Quinn and Brannon, 1982), making it functionally different from the magnetic compasses of birds (Wiltschko and Wiltschko, 1972) and sea turtles (Light et al., 1993; Goff et al., 1998). Polarity compasses have properties consistent with magnetite but are incompatible with chemical magnetoreception (Johnsen and Lohmann, 2005; Rodgers and Hore, 2009). It is noteworthy that mole rats and bats also have polarity compasses (Marhold et al., 1997b; Wang et al., 2007) and that the orientation behaviour of these animals is also altered by a magnetic pulse. Thus, a possible interpretation is that salmon, mole rats and bats all have magnetite-based magnetic compasses.

Findings with migratory birds, however, suggest that it is premature to conclude that magnetic pulses necessarily affected the salmon compass, inasmuch as similar magnetic pulses are thought to primarily affect a map sense in birds (Wiltschko and Wiltschko, 1995b, 2003; Holland and Helm, 2013). In birds, juveniles making their first migration are thought to lack map information and guide themselves by maintaining a compass heading, whereas adults exploit a map acquired from previous migratory experience (Wiltschko and Wiltschko, 2003). Interestingly, the effect of a magnetic pulse was restricted to experienced birds that had already completed at least one migration, whereas naive birds were unaffected by the same pulse (Munro et al., 1997; Wiltschko et al., 1998). For salmon, further studies will be needed to determine precisely what parts of the salmon magnetoreception and navigation system are affected by a magnetic pulse.

Comparison with previous salmon studies

In part of our study, juvenile Chinook salmon were exposed to a magnetic field that exists near the southern periphery of their oceanic range. In a previous experiment with Chinook salmon, this field elicited northward orientation (Putman et al., 2014a), but in the present study, control fish tested in this same field had orientation indistinguishable from random. The reason for this difference is not known. A possible explanation, however, is that fish used in this study were younger and originated from the Elk River, which enters the Pacific approximately 400 km south of the entry point of fish used previously (Putman et al., 2014a). Chinook salmon populations are known to vary in their oceanic distribution (Weitkamp, 2010) and thus presumably have different oceanic boundaries. An interesting possibility is that different salmon populations have different responses to magnetic fields, with each population responding most strongly to combinations of intensity and inclination angle that represent boundaries for that group (Putman et al., 2014a). A wider survey of magnetic orientation responses across Chinook populations and through ontogeny is required before firm conclusions can be drawn.

Another methodological difference between the present study and that of Putman et al. (2014a) is that all fish in our study, including controls, were briefly placed in a solenoid prior to testing in a magnetic coil. Although control fish were not exposed to a magnetic pulse, they were nevertheless exposed to an altered magnetic field with a different inclination and intensity immediately before testing. Fish in the solenoid experienced a change in field intensity of approximately 0.8 μT (approximately 1.5% of the local field), with the effect on inclination being difficult to measure. Whether this brief exposure to an altered field affected subsequent behaviour is not known, but longer exposures to stronger magnetic distortions reduce the ability of salmonids to respond with directed orientation to magnetic displacements (Putman et al., 2014b).

As noted previously, magnetic pulse experiments have been conducted using a variety of different animals and a number of different methodologies. One potential complication of such studies is that a magnetic pulse is inevitably accompanied by a transient electric field; thus, in principle, either the magnetic pulse or the electric field might produce an effect. Some studies have attempted to control for possible effects of the transient electric field by administering pulsed fields while the animal is in a strong 'biasing' magnetic field oriented in one of two directions (e.g. Wiltschko et al., 2002; Holland et al., 2008; Holland and Helm, 2013). By contrast, other studies have not used biasing fields (e.g. Beason et al., 1995; Wiltschko et al., 1998; Wiltschko et al., 2007; Ernst and Lohmann, 2016), including the present one. No obvious difference has emerged between studies using biasing fields and those that have not, inasmuch as pulsed fields affected subsequent orientation behaviour in both methodologies. Nevertheless, additional studies using a variety of experimental designs may be worthwhile in both fish and other animals.

Regardless of these considerations, the pulsed fish and control fish in the present study had significantly different orientation when tested in the magnetic field of a distant ocean location (Fig. 4C,D). This study provides the first evidence linking a magnetic pulse to behavioural changes in fish, adding salmon to the growing list of taxa affected by magnetic pulses. The finding that magnetic pulses alter orientation behaviour of salmon is consistent with the hypothesis that magnetoreceptors in teleost fish are based on magnetite crystals. Further research will be needed to confirm or refute this hypothesis and to definitively characterize the mechanisms that underlie magnetoreception in animals.

Acknowledgements

We thank M. Anguelov, C. Jackson, M. Xiong, L. Roberson, M. Hankins and S. Ataei for assisting with the photo analysis, and members of the Lohmann lab for comments on experimental design and manuscript drafts. We also thank J. O'Neil, J. Krajcik and A. Powell of the Oregon Hatchery Research Center for assisting with the fish husbandry.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.C.N.-J., N.F.P., K.J.L.; Methodology: L.C.N.-J., N.F.P., K.J.L.; Validation: L.C.N.-J., K.J.L.; Formal analysis: L.C.N.-J.; Investigation: L.C.N.-J., N.F.P., M.M.S.; Resources: L.C.N.-J., M.M.S., D.L.G.N., K.J.L.; Writing - original draft: L.C.N.-J., K.J.L.; Writing - review & editing: L.C.N.-J., N.F.P., M.M.S., D.L.G.N., K.J.L.; Visualization: L.C.N.-J., K.J.L.; Supervision: N.F.P., D.L.G.N., K.J.L.; Project administration: L.C.N.-J., N.F.P., M.M.S., D.L.G.N., K.J.L.; Funding acquisition: D.L.G.N., K.J.L.

Funding

This work was funded in part by grants from the National Science Foundation [IOS-1456923 to K.J.L.], the Air Force Office of Scientific Research [FA9550-14-1-0208 to K.J.L.], the Oregon Hatchery Research Center, and Oregon Department of Fish and Wildlife.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.222091.supplemental

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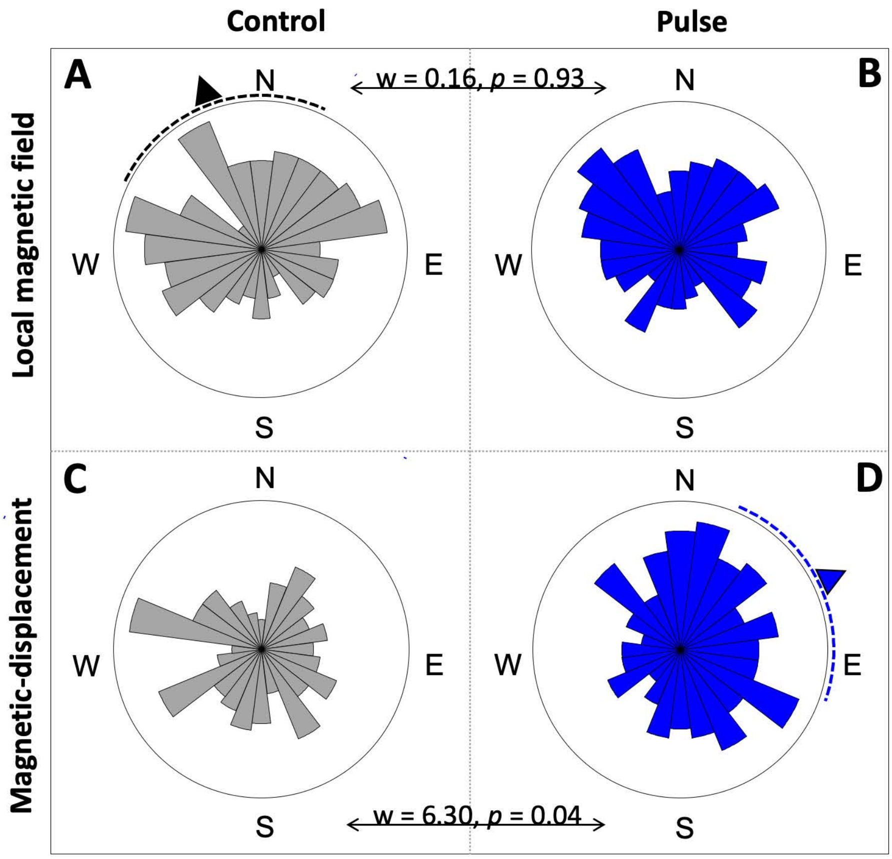

Fig. S1. Analysis of data treating each fish as an independent data point. (A) Under local magnetic field conditions fish from the control group were significantly oriented with a mean angle of 341 deg (Rayleigh test, *n*=208 , *r*=0.12 , *z*=3.20 , p=0.04). (B) Under local magnetic field conditions salmon that experienced a strong magnetic pulse were not oriented as a group (Rayleigh test, *n* =196 , *r* =0.12 , *z* =2.78, *p* =0.06). (C) During a magnetic displacement to a southern ocean region, control fish were not oriented as a group (Rayleigh test, *n* =216 , *r* =0.06 , *z* =0.72 , *p* =0.49) . (D) During the magnetic displacement, salmon from the pulse group were significantly oriented with a mean angle of 66 deg (Rayleigh test, *n* =204 , *r* =0.13, *z* =3.30, *p* =0.04) . The length of each bar indicates the number of fish that were oriented within each 15 degree range of directions. Arrow heads indicate the mean direction of each treatment group. Dotted lines represent the 95% confidence interval for the mean. Fish that we were unable to determine a clear angle of orientation for (due to glare in the photos) were omitted from the analysis, resulting in the slightly uneven sample sizes.

Table S1. Average orientation angle of individual fish. Data shown are for control or pulsed fish tested under local ambient conditions and during a magnetic-displacement to a southern ocean region.

Trial#	Treatment	Ambient	Magnetic-displacement
T1	Control	6.0	191.2
T2	Pulse	52.4	135.7
T3	Control	20.6	267.6
T4	Pulse	227.9	55.0
T5	Control	295.5	356.7
T6	Pulse	70.5	215.3
T7	Control	357.0	115.0
T8	Pulse	266.4	118.9
T9	Control	304.7	169.1
T10	Pulse	53.0	11.7
T11	Control	72.0	314.1
T12	Pulse	199.4	163.3
T13	Control	30.8	126.9
T14	Pulse	294.4	50.9
T15	Control	327.4	141.9
T16	Pulse	24.1	54.4
T17	Control	322.2	288.3
T18	Pulse	26.1	336.3
T19	Control	331.2	11.8
T20	Pulse	300.6	15.9
T21	Control	351.3	137.0
T22	Pulse	312.6	114.7
T23	Control	164.5	254.9
T24	Pulse	54.9	90.2
T25	Control	215.0	122.7
T26	Pulse	321.4	38.3
T27	Control	284.5	310.5

Table S2. Average orientation angle of indidual fish. Data shown are for control or pulsed fish tested under local ambient conditions and during a magnetic-displacement to a southern ocean region.

Trial #	Treatment	Bucket#	Ambient	Magnetic-displacement
T1	Control	1	334.3	141.7
T1	Control	2	8.1	181.9
T1	Control	3	129.4	157.5
T1	Control	4	47.8	122.8
T1	Control	5	NA	242.8
T1	Control	6	68.4	319.0
T1	Control	7	51.6	77.8
T1	Control	8	335.2	300.9
T1	Control	9	324.7	288.1
T1	Control	10	25.6	178.0
T1	Control	11	168.9	268.5
T1	Control	12	345.1	113.9
T1	Control	13	189.2	168.3
T1	Control	14	255.0	156.5
T1	Control	15	14.6	191.8
T1	Control	16	304.5	286.2
T2	Pulse	1	115.8	76.3
T2	Pulse	2	286.8	250.2
T2	Pulse	3	316.7	99.2
T2	Pulse	4	52.2	141.1
T2	Pulse	5	346.7	313.9
T2	Pulse	6	112.2	227.7
T2	Pulse	7	37.7	175.5
T2	Pulse	8	337.2	322.3
T2	Pulse	9	NA	230.3
T2	Pulse	10	316.8	74.7
T2	Pulse	11	101.5	106.0
T2	Pulse	12	161.8	188.9
T2	Pulse	13	NA	258.4
T2	Pulse	14	50.7	67.4
T2	Pulse	15	139.5	101.3
T2	Pulse	16	83.1	74.4
T3	Control	1	257.1	278.2
T3	Control	2	319.1	347.6
T3	Control	3	28.6	278.9
T3	Control	4	51.3	NA
T3	Control	5	122.0	25.6
T3	Control	6	35.3	242.4
T3	Control	7	217.8	212.1
T3	Control	8	297.6	134.5
T3	Control	9	141.1	0.6
T3	Control	10	326.9	175.5
T3	Control	11	49.0	231.1
T3	Control	12	NA	19.0
T3	Control	13	135.6	288.1
T3	Control	14	112.5	189.0
T3	Control	15	342.6	298.5
T3	Control	16	245.5	238.3
T4	Pulse	1	328.1	322.7
T4	Pulse	2	42.0	6.7
T4	Pulse	3	282.3	235.5

T4	Pulse	4	166.0	108.3
T4	Pulse	5	232.2	331.2
T4	Pulse	6	211.4	46.3
T4	Pulse	7	218.8	175.5
T4	Pulse	8	150.0	121.1
T4	Pulse	9	203.2	149.9
T4	Pulse	10	325.2	105.3
T4	Pulse	11	52.6	263.8
T4	Pulse	12	NA	41.9
T4	Pulse	13	174.3	201.7
T4	Pulse	14	76.1	358.7
T4	Pulse	15	262.7	80.7
T4	Pulse	16	260.7	297.5
T5	Control	1	342.6	227.1
T5	Control	2	44.0	280.1
T5	Control	3	20.8	34.2
T5	Control	4	20.8	350.2
T5	Control	5	270.0	4.5
T5	Control	6	257.0	304.6
T5	Control	7	184.4	332.7
T5	Control	8	188.1	323.2
T5	Control	9	286.8	50.2
T5	Control	10	53.6	149.9
T5	Control	11	133.1	143.3
T5	Control	12	NA	290.0
T5	Control	13	244.2	311.9
T5	Control	14	332.9	54.2
T5	Control	15	214.3	61.7
T5	Control	16	NA	109.2
T6	Pulse	1	204.3	232.9
T6	Pulse	2	22.1	151.1
T6	Pulse	3	318.3	292.8
T6	Pulse	4	83.8	48.3
T6	Pulse	5	54.0	346.4
T6	Pulse	6	71.8	204.6
T6	Pulse	7	140.1	322.1
T6	Pulse	8	341.1	116.4
T6	Pulse	9	110.5	190.2
T6	Pulse	10	86.2	123.1
T6	Pulse	11	56.0	203.5
T6	Pulse	12	304.8	275.0
T6	Pulse	13	190.7	326.7
T6	Pulse	14	238.5	120.8
T6	Pulse	15	303.6	236.9
T6	Pulse	16	183.3	202.0
T7	Control	1	23.2	234.3
T7	Control	2	238.8	107.6
T7	Control	3	82.4	27.9
T7	Control	4	116.1	334.7
T7	Control	5	220.9	211.1
T7	Control	6	251.5	121.1
T7	Control	7	103.3	289.9

T7	Control	8	164.0	93.7
T7	Control	9	335.0	96.6
T7	Control	10	1.5	174.0
T7	Control	11	3.9	52.1
T7	Control	12	NA	15.4
T7	Control	13	290.8	252.6
T7	Control	14	1.9	160.8
T7	Control	15	248.0	248.8
T7	Control	16	94.3	69.7
T8	Pulse	1	133.7	88.9
T8	Pulse	2	54.0	319.9
T8	Pulse	3	199.3	184.9
T8	Pulse	4	191.6	127.5
T8	Pulse	5	113.9	48.0
T8	Pulse	6	260.8	10.7
T8	Pulse	7	320.1	129.2
T8	Pulse	8	3.5	82.9
T8	Pulse	9	NA	157.7
T8	Pulse	10	284.5	60.6
T8	Pulse	11	161.9	264.6
T8	Pulse	12	36.1	NA
T8	Pulse	13	274.2	291.7
T8	Pulse	14	331.2	193.4
T8	Pulse	15	301.0	119.4
T8	Pulse	16	205.6	257.5
T9	Control	1	NA	NA
T9	Control	2	295.5	156.6
T9	Control	3	358.2	194.8
T9	Control	4	177.5	178.1
T9	Control	5	NA	291.7
T9	Control	6	282.3	215.3
T9	Control	7	72.5	23.7
T9	Control	8	24.9	NA
T9	Control	9	269.0	91.1
T9	Control	10	114.6	305.9
T9	Control	11	297.7	195.6
T9	Control	12	263.4	43.9
T9	Control	13	355.1	323.1
T9	Control	14	168.7	156.1
T9	Control	15	97.3	117.7
T9	Control	16	268.8	161.3
T10	Pulse	1	199.7	61.9
T10	Pulse	2	45.5	6.4
T10	Pulse	3	65.5	69.6
T10	Pulse	4	46.0	145.4
T10	Pulse	5	251.6	230.5
T10	Pulse	6	38.7	331.3
T10	Pulse	7	139.3	160.4
T10	Pulse	8	194.4	355.8
T10	Pulse	9	333.5	355.5
T10	Pulse	10	330.4	87.4
T10	Pulse	11	57.0	12.4

T10	Pulse	12	138.6	299.4
T10	Pulse	13	140.7	311.5
T10	Pulse	14	36.0	333.0
T10	Pulse	15	277.0	42.4
T10	Pulse	16	275.3	12.8
T11	Control	1	349.1	146.5
T11	Control	2	258.6	322.1
T11	Control	3	114.0	86.0
T11	Control	4	138.8	12.8
T11	Control	5	101.8	230.8
T11	Control	6	111.6	196.1
T11	Control	7	230.2	245.2
T11	Control	8	98.5	205.6
T11	Control	9	277.0	208.7
T11	Control	10	54.5	17.1
T11	Control	11	60.3	30.8
T11	Control	12	45.8	64.4
T11	Control	13	34.6	289.7
T11	Control	14	57.9	279.4
T11	Control	15	76.8	7.9
T11	Control	16	269.4	99.2
T12	Pulse	1	160.1	314.8
T12	Pulse	2	303.0	176.2
T12	Pulse	3	218.5	74.9
T12	Pulse	4	132.3	78.7
T12	Pulse	5	211.3	354.0
T12	Pulse	6	167.4	188.8
T12	Pulse	7	6.1	89.3
T12	Pulse	8	103.5	216.2
T12	Pulse	9	255.4	146.3
T12	Pulse	10	214.0	281.0
T12	Pulse	11	298.5	183.1
T12	Pulse	12	349.5	133.9
T12	Pulse	13	52.5	338.7
T12	Pulse	14	116.6	326.3
T12	Pulse	15	181.7	277.5
T12	Pulse	16	237.5	132.4
T13	Control	1	49.3	97.8
T13	Control	2	331.8	150.4
T13	Control	3	194.2	50.4
T13	Control	4	75.6	73.2
T13	Control	5	91.4	188.5
T13	Control	6	284.7	250.3
T13	Control	7	127.1	40.1
T13	Control	8	7.3	121.9
T13	Control	9	11.2	226.4
T13	Control	10	127.6	144.7
T13	Control	11	283.7	238.7
T13	Control	12	53.6	76.3
T13	Control	13	28.8	130.4
T13	Control	14	156.7	164.2
T13	Control	15	323.4	312.8

T13	Control	16	327.0	75.7
T14	Pulse	1	68.3	352.9
T14	Pulse	2	234.0	3.8
T14	Pulse	3	248.4	348.8
T14	Pulse	4	291.2	166.0
T14	Pulse	5	NA	NA
T14	Pulse	6	122.1	74.0
T14	Pulse	7	154.4	96.1
T14	Pulse	8	328.3	138.3
T14	Pulse	9	325.6	270.0
T14	Pulse	10	106.6	235.5
T14	Pulse	11	249.5	356.6
T14	Pulse	12	10.3	54.1
T14	Pulse	13	NA	22.1
T14	Pulse	14	101.2	261.5
T14	Pulse	15	19.2	144.0
T14	Pulse	16	202.1	117.6
T15	Control	1	182.0	8.3
T15	Control	2	323.4	51.1
T15	Control	3	235.0	59.8
T15	Control	4	309.8	127.0
T15	Control	5	292.1	151.3
T15	Control	6	157.4	258.9
T15	Control	7	23.3	313.5
T15	Control	8	289.9	116.4
T15	Control	9	NA	316.8
T15	Control	10	51.0	162.7
T15	Control	11	101.0	139.2
T15	Control	12	63.5	230.4
T15	Control	13	303.6	279.4
T15	Control	14	111.0	58.1
T15	Control	15	356.5	153.9
T15	Control	16	260.8	208.3
T16	Pulse	1	360.0	61.0
T16	Pulse	2	347.0	5.3
T16	Pulse	3	237.5	81.9
T16	Pulse	4	77.1	41.4
T16	Pulse	5	285.9	98.6
T16	Pulse	6	145.3	197.6
T16	Pulse	7	96.8	123.6
T16	Pulse	8	78.3	352.2
T16	Pulse	9	345.6	21.3
T16	Pulse	10	94.7	37.9
T16	Pulse	11	3.6	250.0
T16	Pulse	12	32.7	210.3
T16	Pulse	13	50.0	11.9
T16	Pulse	14	4.7	352.0
T16	Pulse	15	274.9	189.5
T16	Pulse	16	15.3	91.4
T17	Control	1	284.7	337.4
T17	Control	2	1.4	207.7
T17	Control	3	12.2	142.2

T17	Control	4	275.1	315.0
T17	Control	5	237.2	195.0
T17	Control	6	174.5	173.7
T17	Control	7	10.5	239.1
T17	Control	8	213.7	35.6
T17	Control	9	67.1	246.7
T17	Control	10	322.8	271.7
T17	Control	11	332.4	35.9
T17	Control	12	8.3	31.7
T17	Control	13	58.4	238.7
T17	Control	14	NA	350.3
T17	Control	15	275.4	36.1
T17	Control	16	169.9	NA
T18	Pulse	1	2.4	284.8
T18	Pulse	2	333.7	179.5
T18	Pulse	3	143.4	116.5
T18	Pulse	4	122.1	103.3
T18	Pulse	5	58.9	27.9
T18	Pulse	6	243.1	247.0
T18	Pulse	7	61.4	164.7
T18	Pulse	8	70.3	149.4
T18	Pulse	9	308.9	321.5
T18	Pulse	10	298.5	40.1
T18	Pulse	11	310.1	313.6
T18	Pulse	12	60.2	346.1
T18	Pulse	13	208.6	353.8
T18	Pulse	14	44.1	28.4
T18	Pulse	15	31.0	234.7
T18	Pulse	16	33.6	302.5
T19	Control	1	352.1	240.6
T19	Control	2	187.9	36.2
T19	Control	3	51.5	71.7
T19	Control	4	302.5	78.7
T19	Control	5	70.9	301.9
T19	Control	6	348.3	278.0
T19	Control	7	341.8	277.9
T19	Control	8	16.1	98.6
T19	Control	9	128.0	250.7
T19	Control	10	244.7	8.2
T19	Control	11	253.5	48.6
T19	Control	12	76.5	302.5
T19	Control	13	347.8	246.7
T19	Control	14	287.3	130.5
T19	Control	15	303.8	144.0
T19	Control	16	223.7	120.7
T20	Pulse	1	NA	305.1
T20	Pulse	2	133.9	147.6
T20	Pulse	3	295.8	51.5
T20	Pulse	4	117.3	267.4
T20	Pulse	5	180.0	145.9
T20	Pulse	6	131.9	72.8
T20	Pulse	7	3.5	3.5

T20	Pulse	8	34.4	22.2
T20	Pulse	9	270.5	202.2
T20	Pulse	10	245.3	16.9
T20	Pulse	11	291.2	294.2
T20	Pulse	12	277.2	337.8
T20	Pulse	13	305.7	26.3
T20	Pulse	14	17.7	322.3
T20	Pulse	15	314.9	41.2
T20	Pulse	16	NA	121.8
T21	Control	1	NA	50.5
T21	Control	2	76.1	241.2
T21	Control	3	2.6	245.6
T21	Control	4	82.2	185.9
T21	Control	5	249.4	216.0
T21	Control	6	302.0	335.6
T21	Control	7	51.1	190.3
T21	Control	8	NA	12.9
T21	Control	9	119.4	88.9
T21	Control	10	222.3	98.4
T21	Control	11	333.9	126.8
T21	Control	12	326.2	60.4
T21	Control	13	8.8	200.7
T21	Control	14	179.3	90.8
T21	Control	15	221.4	310.0
T21	Control	16	NA	322.0
T22	Pulse	1	6.7	111.8
T22	Pulse	2	319.9	12.3
T22	Pulse	3	212.8	52.4
T22	Pulse	4	255.9	33.2
T22	Pulse	5	290.8	342.9
T22	Pulse	6	245.2	171.2
T22	Pulse	7	311.5	258.1
T22	Pulse	8	NA	240.6
T22	Pulse	9	97.4	185.2
T22	Pulse	10	32.6	171.0
T22	Pulse	11	304.1	27.2
T22	Pulse	12	NA	123.9
T22	Pulse	13	77.6	85.0
T22	Pulse	14	27.4	122.0
T22	Pulse	15	219.9	171.7
T22	Pulse	16	NA	NA
T23	Control	1	87.1	286.2
T23	Control	2	198.3	67.3
T23	Control	3	275.2	307.3
T23	Control	4	76.4	29.7
T23	Control	5	97.2	231.1
T23	Control	6	268.8	45.5
T23	Control	7	84.9	198.4
T23	Control	8	NA	NA
T23	Control	9	170.5	244.6
T23	Control	10	110.0	264.4
T23	Control	11	240.5	235.1

T23	Control	12	235.5	179.7
T23	Control	13	242.1	228.9
T23	Control	14	266.7	280.4
T23	Control	15	72.1	250.5
T23	Control	16	116.5	NA
T24	Pulse	1	8.1	59.9
T24	Pulse	2	106.0	58.1
T24	Pulse	3	118.1	19.3
T24	Pulse	4	184.1	165.8
T24	Pulse	5	30.0	NA
T24	Pulse	6	35.5	121.7
T24	Pulse	7	9.4	148.7
T24	Pulse	8	291.4	26.2
T24	Pulse	9	332.3	140.7
T24	Pulse	10	209.0	35.3
T24	Pulse	11	280.3	26.6
T24	Pulse	12	110.1	209.9
T24	Pulse	13	128.2	263.5
T24	Pulse	14	66.5	131.5
T24	Pulse	15	292.1	127.0
T24	Pulse	16	100.2	319.9
T25	Control	1	67.1	308.6
T25	Control	2	290.2	91.4
T25	Control	3	247.3	29.6
T25	Control	4	78.6	NA
T25	Control	5	202.6	221.2
T25	Control	6	58.6	138.8
T25	Control	7	250.4	3.3
T25	Control	8	NA	21.1
T25	Control	9	177.5	110.1
T25	Control	10	284.7	297.3
T25	Control	11	77.5	112.3
T25	Control	12	202.6	NA
T25	Control	13	227.0	180.8
T25	Control	14	222.0	168.9
T25	Control	15	NA	121.9
T25	Control	16	214.4	195.3
T26	Pulse	1	314.4	21.1
T26	Pulse	2	293.5	317.1
T26	Pulse	3	313.9	151.2
T26	Pulse	4	342.4	36.8
T26	Pulse	5	22.0	220.4
T26	Pulse	6	176.4	168.7
T26	Pulse	7	299.2	206.4
T26	Pulse	8	122.6	18.0
T26	Pulse	9	313.6	172.7
T26	Pulse	10	53.6	351.0
T26	Pulse	11	250.0	241.3
T26	Pulse	12	316.4	93.7
T26	Pulse	13	336.8	337.5
T26	Pulse	14	265.9	154.8
T26	Pulse	15	18.9	31.2

T26	Pulse	16	NA	7.9
T27	Control	1	215.1	147.7
T27	Control	2	308.5	206.0
T27	Control	3	338.6	338.1
T27	Control	4	242.8	127.3
T27	Control	5	125.3	7.5
T27	Control	6	155.3	69.9
T27	Control	7	60.3	332.6
T27	Control	8	285.6	284.7
T27	Control	9	283.4	302.8
T27	Control	10	28.3	288.8
T27	Control	11	301.1	340.4
T27	Control	12	NA	78.7
T27	Control	13	280.1	136.5
T27	Control	14	175.2	305.5
T27	Control	15	263.8	183.6
T27	Control	16	35.3	266.5

NA =instances when capturing fish orientation was not possible.