Potential Role of the Magnetic Field on Homing in Chum Salmon (*Oncorhynchus keta*) Tracked from the Open Sea to Coastal Japan

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Abstract: In order to examine the Earth's magnetic intensity and inclination during homing migration of chum salmon (*Oncorhynchus keta*) and to present tracking data consistent with the geomagnetic imprinting hypothesis that salmon migrate homeward using the Earth's magnetic intensity or inclination, archival tagging operations were carried out in the Bering Sea in 2012 and 2013. DST magnetic tags were attached to the bodies of chum salmon on board a research ship. The tags recorded temperature, depth, magnetic intensity and inclination, compass heading, and tilt of the fish. Two tagged chum salmon were subsequently recovered near the coast of Hokkaido, Japan, in 2012 and 2013, respectively. The estimated homing route of the 2012 fish was linear from the release site to the coast of Hokkaido, Japan. The 2013 fish reached the coast of Hokkaido by way of the east coast of Kamchatka, Russia. These estimated homing routes were not consistent with the great circle route. The estimated homing migration routes were consistent with the isoline of magnetic intensity rather than magnetic inclination. For the tag recovered in 2012, the homing migration route was approximately along the isoline of magnetic intensity at the recovery site. Therefore, we conclude that this study supports the geomagnetic imprinting hypothesis that magnetic intensity plays an important role in the homing migration of chum salmon in the open sea.

Keywords: chum salmon, magnetic intensity and inclination, homing migration, archival tag

INTRODUCTION

Chum salmon *(Oncorhynchus keta)* of Japanese origin remain in the North Pacific Ocean and the Bering Sea for 1–7 yr before returning to spawn in their natal rivers. Urawa (2000, 2004) constructed a model of the ocean life of Japanese chum salmon using genetic stock identification methods. They indicated that in spring Japanese chum salmon released in Hokkaido spend three months at the coast of the Okhotsk Sea and remain in the Okhotsk Sea until late fall. At ocean age-2 they migrate eastward from the western North Pacific Ocean to the central North Pacific Ocean during winter and spring, and enter the Bering Sea the following summer. In the autumn they move into the Gulf of Alaska in the eastern North Pacific to spend the winter. They repeat the Bering Sea to the eastern North Pacific Ocean migration 3–4 times. When they are ready to mature in the summer of their fourth/fifth year, they return to their natal rivers in Hokkaido, Japan.

Studies of chum salmon using archival tags have determined the characteristics of swimming patterns and ambient environmental conditions during homing migrations (Wada and Ueno 1999; Tanaka et al. 2000; Walker et al. 2000; Friedland et al. 2001; Ishida et al. 2001; Azumaya and Ishida 2005). These studies showed that diel vertical movements were pronounced in the open ocean. Chum salmon remained near the surface at night, but they showed short-term vertical movements lasting < 1 hour during the day. However, archival tagging operations that record the magnetic field to which homing chum salmon are exposed have not been carried out.

Several animals are known to determine their geographic position using information in the Earth's magnetic field (Lohman et al. 2007; Putman et al. 2014). Quinn (1980) and

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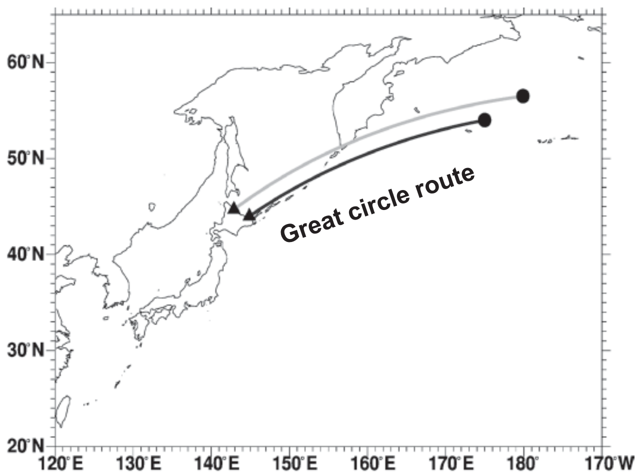

Fig. 1. Release (black circles) and recovery sites (black triangles) and great circle route for Fish 608 (gray) and Fish 669 (black).

Quinn and Brannon (1982) showed that juvenile sockeye salmon *(O. nerka)* in tanks oriented along the axis of their natal lake changed direction in response to induced magnetic fields. The responses to induced fields only occurred at night or in covered tanks, but not during the day with tanks open to the sky. They indicated that sockeye salmon can use the Earth's magnetic field to determine compass direction and suggested that juvenile salmon imprint on the magnetic field before heading to sea. Quinn (1984) proposed that oceanic migrating salmon have a 'magnetic map sense' based on the inclination and declination of the Earth's magnetic field. To investigate the role of magnetic compass orientation in oceanic migrating chum salmon, Yano et al. (1997) fitted chum salmon with a tag that generated an artificial magnetic field. He then modified the geomagnetic field around the heads of fish and observed their orientation and swimming speed. Their results suggested that the orientation of the tracked chum salmon was not significantly affected by a modified magnetic field.

According to the geomagnetic imprinting hypothesis (Lohmann et al. 2008; Bracis and Anderson 2012**)**, the difference between the imprinted geomagnetic value and that at a salmon's ocean location can potentially guide its homeward migration such that salmon navigate homeward from oceanic habitats by comparing properties of the Earth's magnetic field at their immediate location to those on which they were imprinted as juveniles entering the ocean. Bracis and Anderson (2012), Putman et al. (2013), and Putman et al. (2014), using a migration model or statistics, showed that salmon used the Earth's magnetic intensity to find their way back to their birthplace after migrating across thousands of miles of open sea. However, it has not yet been confirmed that salmon experience the Earth's magnetic fields during homing migration. Thus, the aims of the present study were to investigate the possible role of magnetic orientation during the oceanic migration of maturing chum salmon. We conducted archival tagging operations that could record the magnetic field in the Bering Sea and examined features of magnetic intensity that chum salmon experienced during homing migration. We present tracking data that is consistent with the geomagnetic imprinting hypothesis.

MATERIALS AND METHODS

DST magnetic tags (Star-Oddi, Gardabaer, Iceland) were attached to the bodies of chum salmon on board the research vessel *Hokko maru* in 2012 and 2013. The chum salmon carrying tag 608 (hereafter Fish 608) was caught in 2012 by hook and line, and after twelve tagged chum salmon were released in the central Bering Sea (56°28'N, 179°54'E; Fig. 1). At tagging, the fork length of Fish 608 was measured as 650 mm. Fish 608 was recovered along the coast of Hokkaido, Japan (44°40'N, 142°52'E) 74 days after release in 2012 (Table 1). The chum salmon carrying tag 669 (hereafter Fish 669) was caught in 2013 by surface trawl, and after six tagged chum salmon were released in the central Bering Sea (54°01'N, 175°05'E; Fig. 1). At tagging, the fork length of Fish 669 was measured as 613 mm. Fish 669 was recovered along the coast of Hokkaido, Japan (43°59', 144°52'E) 76 days after release in 2013 (Table 1).

The DST was 15 mm in diameter, 46 mm in length, and 19 g (12 g) in air (water). The housing material was alumina (ceramic). The tags measured and recorded magnetic field strength, tilt of the fish, compass heading, temperature and pressure (depth) every 60 minutes for Fish 608 and every 10

Table 1. Release and recapture information for two chum salmon tagged with archival tags in the Bering Sea and recovered in Hokkaido, Japan. Days at liberty: days between release and recovery. Distance: shortest distance between release and recovery sites. Age was determined from scales (Ito and Ishida 1998). FL = fork length.

Fish No.	Release					Recapture							
	Date	Location	Region	FL (mm)	Age	Date	Location	Region	FL (mm)	Days at liberty	Distance (km)	Sex	Swimming speed (m/s)
608	July 30 2012	56°28'N, 179°54'E	Bering Sea	650	-	Oct 11 2012	44°40'N, 142°52'E	Oumu coast	605	74	2,875	male	0.462
669	July 26 2013	54°01'N, 175°05'E	Bering Sea	613	4	Oct 9 2013	43°59'N, 144°52'E	Shari coast	635	76	2,439	female	0.376

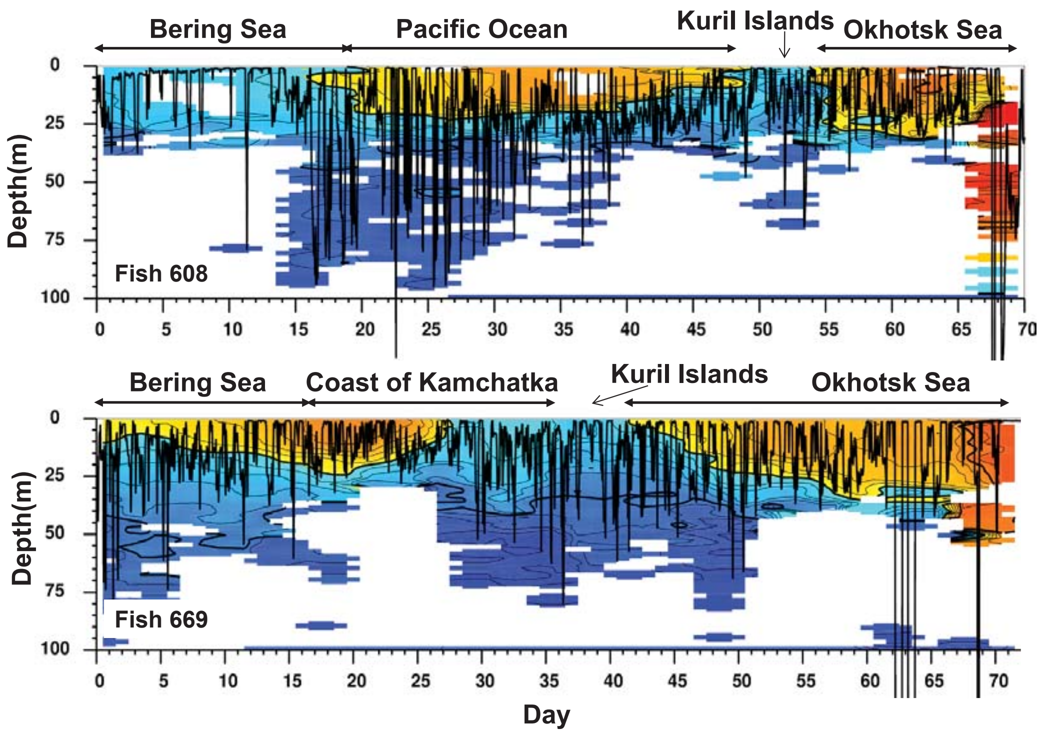

Fig. 2. Time-space diagram of water temperatures. Shades of blue indicate temperatures < 10°C, yellow and red indicate temperatures > 10°C. The thin contour line interval is1°C and the thick contour interval is 5°C. The black lines represent swimming depth. The X-axis represents days after release. The Y-axis represents depth. The upper panel displays data for Fish 608 and the lower panel displays data for Fish 669.

minutes for Fish 669. Temperature readings had a resolution of 0.1°C, depth had a resolution of 0.08 m, and tilt had a resolution of 0.2°. Compass resolution was 1° and magnetic intensity resolution was 30 nT.

The homing route was estimated using temperature and magnetic field data collected and stored in the tag; daily SST data were available from NOAA (www.esrl.noaa.gov/psd/data/gridded/) and the magnetic field data were provided by the Enhanced Magnetic Model (www.ngdc.noaa.gov/geomag/EMM/). Daily SST and magnetic field data were provided for 0.25° X 0.25° grid. The grid positions, where daily mean temperature, magnetic inclination and intensity at less than a depth of 5 m recovered from the tag were compared with the daily SST and magnetic field data, respectively, to identify the possible homing migration route.

To investigate whether the homing migration route depended on the magnetic fields, we calculated the distance between the latitude of each of the estimated homing migration positions and that of the isoline of magnetic intensity or inclination. The same method was performed for all estimated homing migration positions. The mean of these calculated distances was defined as the meridional distance between the migration route and the isoline. If the meridional distance is shorter, the estimated homing route will be near the isoline of magnetic intensity or inclination.

RESULTS AND DISCUSSION

Shortest (great circle route) distance and periods between release and recovery sites for Fish 608 and Fish 669 were 2,875 km and 2,439 km, and 74 days and 76 days, respectively (Fig. 1; Table 1). The horizontal velocities calculated from the positions of release and recovery were

Table 2. Statistics gathered from archived tags placed on two maturing chum salmon released in the Bering Sea and recovered in Hokkaido, Japan. Min = minimum value, Max = maximum value, and SD = standard deviation.

	Temp. (°C)	Depth (m)	Compass Heading (degree)	Inclination (degree)	Intensity (nT)
Fish 608					
Min	1.27	0.83	3	36	46765
Mean	9.65	28.82	237.7	63.19	51106
Max	19.77	173.51	360	84	55496
SD	3.61	21.13	60.31	5.95	1091.36
Fish 669					
Min	0.07	0.77	0	-83	48560
Mean	10.24	17.06	22.6	60.13	51509
Max	16.55	276.93	360	89	56617
SD	3.05	34.13	113.06	25.47	756.69

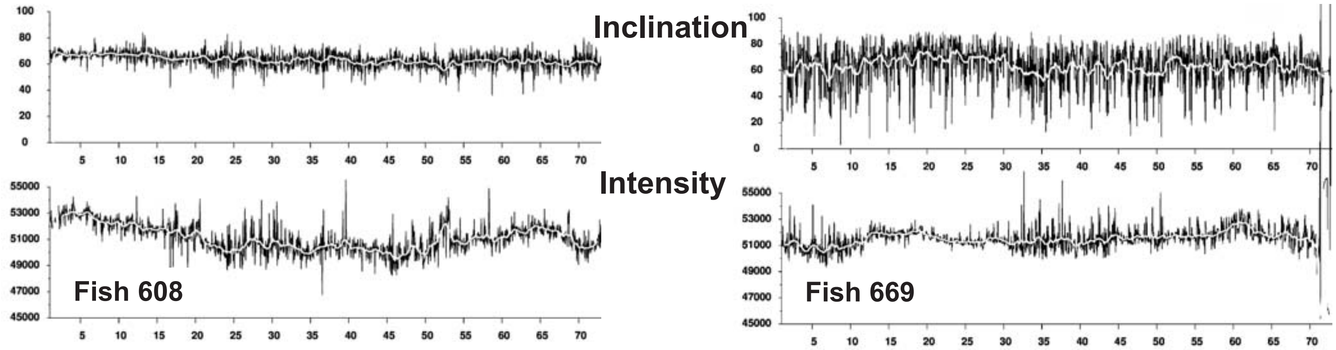

Fig. 3. Time series of raw data from archival tags (black lines) and 25-hour running means (white lines). The X-axis represents days after release. The upper panel is the magnetic inclination (degree) and the lower panel is the magnetic intensity (nT). Left panel displays data for Fish 608 and the right panel displays data for Fish 669.

0.46 m/s and 0.38 m/s, respectively. These velocities were similar to the values of 0.359–0.475 m/s in Azumaya and Ishida (2005). Pronounced oscillatory diving was observed and chum salmon dived under the thermocline during the day (Fig. 2). The chum salmon seem to dive deeper in areas with relatively high sea surface temperatures, e.g., the western North Pacific and the Okhotsk Sea. These behaviors were also similar to those in previous studies (Wada and Ueno 1999; Walker et al. 2000; Azumaya and Ishida 2005).

The mean magnetic inclination during the homing migration for Fish 608 and Fish 669 was 63.2° and 60.1°, respectively, and the mean magnetic intensity for Fish 608 and Fish 669 was 51106 nT and 51509 nT, respectively (Table 2). The SD of magnetic inclination of Fish 608 (SD = 6°) was smaller than that of Fish 669 (SD = 25°; Table 2). Magnetic inclination of Fish 608 was almost constant, but that of Fish 669 fluctuated (Fig. 3). However, the magnetic inclination of Fish 608 had a decreasing trend ($y = -0.0041x + 66.77$; y: inclination, x: day). On the other hand, SD of magnetic intensity of Fish 608 (SD = 1091 nT) was larger than that of Fish 669 (SD = 757 nT; Table 2). The magnetic intensity of Fish 608 fluctuated and that of Fish 669 was almost constant (Fig. 3).

The mean compass heading vector of Fish 608 was 237.7° and that of Fish 669 was 22.6° (Fig. 4; Table 2). Around the Kuril Islands, the compass heading vector of Fish 608 abruptly changed from southwest to northwest on 50th day after release. The mean compass heading vector of Fish 608 was southwestward from the central Bering Sea to the coast of Hokkaido. Although the mean compass heading vector of Fish 669 was not evident from the Bering Sea to the coast of Hokkaido, Fish 669 eventually reached the coast of Hokkaido. Thus, we calibrated the vector of the compass

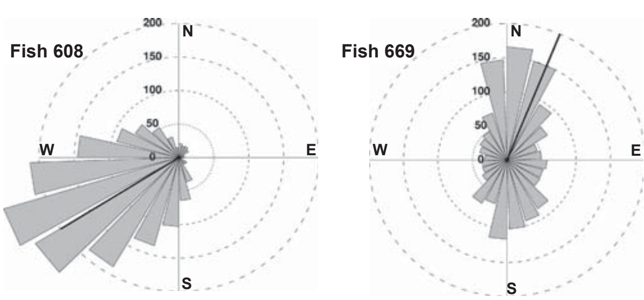

Fig. 4. Frequency of compass headings (gray bars). Black lines indicate the mean direction. Left graph displays data for Fish 608 and the right graph diaplays data for Fish 669.

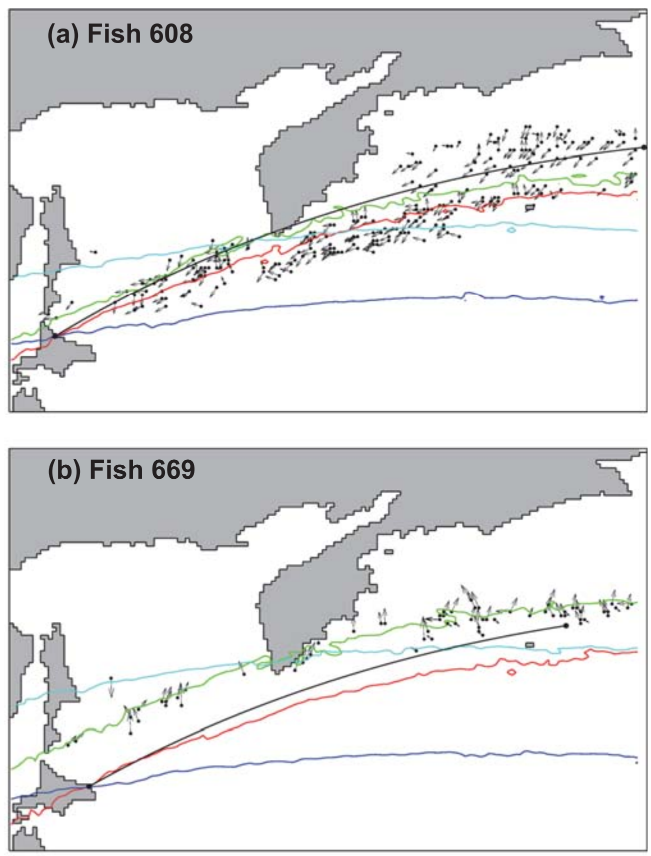

Fig. 5. Horizontal distributions of the homing routes (dots) of Fish 608 (a) and Fish 669 (b) from the Bering Sea to the coast of Hokkaido Japan, the great circle route (black line) and the isolines of the magnetic inclination (blue and light blue lines) and intensity (red and green lines). Arrows indicate the compass heading vector. Blue and red lines indicate the isolines of the magnetic inclination and intensity at the recovery site, respectively. Light blue and green lines indicate isolines of the mean experienced magnetic inclination and intensity, respectively.

heading from data recovered from the tags of Fish 608 and Fish 669 in our laboratory. The RMS (root mean square) of the compass heading for Fish 608 was 14.68° and that for Fish 669 was 23.09°, respectively. The RMS for Fish 669 pointing northward was more than 50°. This indicates that the value of the compass heading of Fish 669 includes inconsistent errors.

Figure 5 shows the estimated homing routes (dots) for Fish 608 and Fish 669 with the compass heading vector. The estimated homing route of Fish 608 was a direct linear movement from the release site to the coast of Hokkaido (Fig. 5(a)). The compass heading vector changed from southwestward in the Bering Sea to west-southwestward in the western North Pacific. Around the Kuril Islands, the compass heading vector of Fish 608 abruptly changed from southwestward to northwestward as previously mentioned. On the other hand, Fish 669 reached the east coast of Kamchatka from the central Bering Sea and moved southward. After that, it moved into the Okhotsk Sea (Fig. 5(b)). However, the compass heading for Fish 669 did not correspond to the estimated homing route because the value of the heading compass of Fish 669 includes error. Velocities of the currents by FRA-ROMS (http://fm.dc.affrc.go.jp/fra-roms/index.html) in the areas from the Bering Sea to the North Pacific Ocean and the Okhotsk Sea were considerably slower than the swimming speed of salmon. Furthermore, directions of the currents were not consistent with the compass heading for Fish 669. Both estimated homing routes of Fish 608 and 669 were not consistent with the great circle route. This suggests that chum salmon did not select the route that was the minimum distance from the Bering Sea to the coast of Hokkaido.

The meridional distances between the estimated homing route and various isolines of magnetic intensity are shown in Figs. 6, 7. The meridional distance from the isoline of magnetic inclination of 65° was the shortest of the various inclinations (Fig. 6) for Fish 608 and Fish 669. The mean experienced magnetic inclination of Fish 608 (solid star) and Fish 669 (open star) did not agree with this value. On the other hand, the meridional distances from the isoline of 51000 nT for Fish 608 and 51500 nT for Fish 669 were the shortest, respectively (Fig. 7). These values corresponded to the value of mean experienced magnetic intensity (solid and open stars). For both Fish 608 and Fish 669, the distance from the isolines of magnetic intensity was shorter than those of the magnetic inclination.

The horizontal distribution of isolines of the mean experienced magnetic inclination (light blue line) and intensity (green line) by chum salmon are shown in Figs. 5(a), (b). The estimated homing route (dots) showed good agreement with the isolines of the mean magnetic intensity rather than the mean magnetic inclination. Thus, these results indicate that chum salmon migrated toward their natal river along the isoline of the magnetic intensity rather than the magnetic inclination.

According to the geomagnetic imprinting hypothesis, salmon navigate homeward by comparing the geomagnetic fields in the ocean with the imprinted ones. Thus, assuming that the recovery site is near their natal river, it is speculated that salmon migrate along the isoline of the magnetic intensity or the inclination of the recovery sites (Bracis and Anderson 2012; Putman et al. 2013). Our results suggest that the estimated homing route for Fish 608 was along the isoline of magnetic intensity (red line; 50540 nT) on the recov-

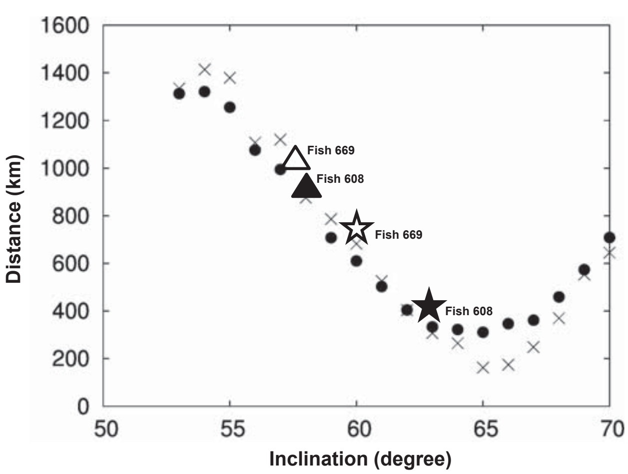

Fig. 6. Meridional distance between the estimated homing route and various isolines of magnetic inclination. The X axis is the magnetic inclination (degree) and the Y axis is distance (km). Dots are for Fish 608 and crosses are for Fish 669. Solid and open stars indicate the mean experienced magnetic inclination for Fish 608 and Fish 669, respectively. Solid and open triangles indicate the magnetic inclination at the recovery site for Fish 608 and Fish 669, respectively.

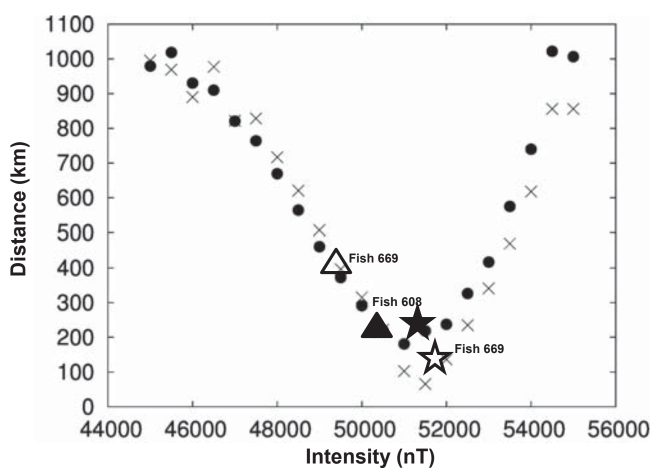

Fig. 7. Meridional distance between the estimated homing route and various isolines of magnetic intensity. The X axis is the magnetic intensity (nT) and the Y axis is distance (km). Dots are for Fish 608 and crosses are for Fish 669. Solid and open stars indicate the mean experienced magnetic intensity for Fish 608 and Fish 669, respectively. Solid and open triangles indicate the magnetic intensity at the recovery site for Fish 608 and Fish 669, respectively.

ery site and meridional distance between estimated homing route and the isoline of the magnetic intensity (50540 nT; solid triangle) was relatively short (Fig. 7). However, the estimated homing route was not consistent with the isoline of magnetic inclination (blue line; 58.5°) on the recovery site (Fig. 5(a)) and meridional distance between estimated homing route and the isoline of the magnetic inclination (58.5°; solid triangle) was relatively long (Fig. 6). It is noted that value of the isoline of magnetic intensity (50540 nT) on the recovery site was near the mean experienced magnetic intensity (51106 nT). This result indicates that salmon migrated homeward using the magnetic intensity at the natal river. On the other hand, the estimated homing route for Fish 669 was not consistent with the isoline of magnetic intensity (red line; 49643 nT) or the isoline of magnetic inclination (blue line; 58.1°) on the recovery site. Meridional distances between estimated homing route and the isoline of the magnetic inclination (58.1°; open triangle) and magnetic intensity (49643 nT; open triangle) on the recovery site were also relatively long as shown in Figs. 6 and 7. However, the estimated homing route for Fish 669 was along the isoline of mean experienced magnetic intensity (green line) and meridional distance between estimated homing route and the isoline of the mean experienced magnetic intensity (51509 nT; open star) was relatively short as previously mentioned (Fig. 7). From this result, it is suggested that the recovery site of Fish 669 was not near its natal river. Chum salmon may not use the magnetic inclination for the homing route in the open sea. However, chum salmon may use it to search for their natal river because their natal river is located around an intersection point of the isolines of magnetic inclination and intensity. Therefore, these results support the geomagnetic imprinting hypothesis.

Although areas of positive SST anomalies in 2012 differed from those in 2013 in the western North Pacific, chum salmon crossed the areas of these positive SST anomalies. Chum salmon migrated homeward along the lines of magnetic intensity both in 2012 and 2013. Thus, the homeward migration route the tagged chum salmon took did not appear to be influenced by the varying SSTs that they swam through. However, in considering their vertical migration, chum salmon have a tendency to dive deeper in areas with relatively high SST (Fig. 2). In addition, Putman et al. (2013) showed that the homing route of sockeye salmon in coastal areas was affected by SST.

In conclusion, we examined the magnetic intensity and inclination experienced during homeward migration of Japanese chum salmon using archival tags to verify the geomagnetic imprinting hypothesis. The tagged chum salmon were released in the central Bering Sea and two tags were recovered along the coast of Hokkaido, Japan. One estimated homing route was linear from the release site to the coast of Japan. The fish using the other homing route reached the coast of Hokkaido by way of the east coast of Kamchatka. These estimated homing routes were not consistent with the great circle route. The present study supports the geomagnetic imprinting hypothesis. We found that magnetic intensity plays an important role in the homing migration of chum salmon in the open sea. Although chum salmon did not use magnetic inclination for finding a homing route in the open sea, chum salmon may use it to search for their natal rivers.

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