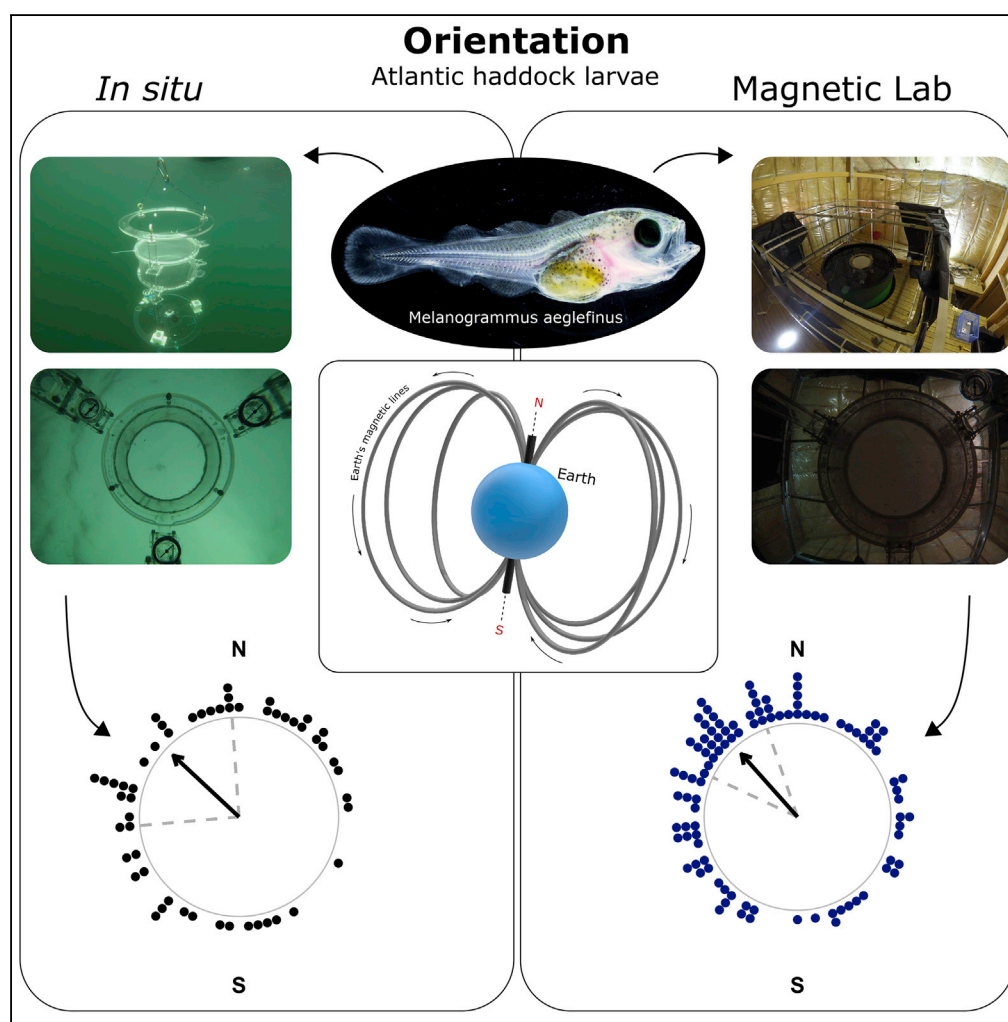


## Article

# Atlantic Haddock (*Melanogrammus aeglefinus*) Larvae Have a Magnetic Compass that Guides Their Orientation



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## HIGHLIGHTS

Atlantic haddock larvae  
drift with the current and  
spread across the North  
Sea

In this area, larvae  
swimming *in situ* orient to  
the northwest

In a magnetic laboratory,  
larvae orient to the same  
direction, the magnetic  
northwest

Haddock larvae have a  
magnetic compass that  
they use to orient at sea

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## Article

# Atlantic Haddock (*Melanogrammus aeglefinus*) Larvae Have a Magnetic Compass that Guides Their Orientation

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## SUMMARY

Atlantic haddock (*Melanogrammus aeglefinus*) is a commercially important species of gadoid fish. In the North Sea, their main spawning areas are located close to the northern continental slope. Eggs and larvae drift with the current across the North Sea. However, fish larvae of many taxa can orient at sea using multiple external cues, including the Earth's magnetic field. In this work, we investigated whether haddock larvae passively drift or orient using the Earth's magnetic field. We observed the behavior of 59 and 102 haddock larvae swimming in a behavioral chamber deployed in the Norwegian North Sea and in a magnetic laboratory, respectively. In both *in situ* and laboratory settings, where the magnetic field direction was modified, haddock larvae significantly oriented toward the northwest. We conclude that haddock larvae orientation at sea is guided by a magnetic compass mechanism. These results have implications for retention and dispersal of pelagic haddock larvae.

## INTRODUCTION

Haddock (*Melanogrammus aeglefinus*) is a species of great ecological and economic importance that has supported a fishery in the North Sea for more than a hundred years (Pope and Macer, 1996). Haddock stocks exhibit large natural fluctuations in abundance on both annual and decadal timescales (Fogarty and Murawski, 1998; Houde, 2016). The main hypotheses explaining such fluctuations, proposed over a century ago, are based on both survival success of the very early life stages and subsequent recruitment (Hjort, 1914). Specifically, Hjort proposed that the fate of year classes depended on a *critical period*, occurring at first feeding of the larvae, during which failure to find prey and to feed would result in high mortality, affecting the abundance of adults during the following years (Hjort, 1914). However, Hjort also proposed that year class success could depend on the dispersal of larvae, and on whether favorable or unfavorable transport of eggs and larvae occurs (Hjort, 1914; Houde, 2016). The meaning of favorable transport varies according to the species, as larvae of some species seek retention in their spawning area, whereas larvae of different species might be advantaged by transport to nursery areas, far from the spawning area. The idea behind Hjort's second hypothesis is that favorable currents, together with appropriate larval behavior, would increase the chances of retention in the nursery areas (or transport to nursery grounds), where the probability of survival is higher (Houde, 2016). The main factor in such retention is the interaction between oceanographic conditions and biological mechanisms, such as larval orientation and swimming (Paris et al., 2013; Paris and Cowen, 2004). At mid-high latitudes, information on swimming and orientation behavior of early life stages of fish is available for only a very few species (Faillietaz et al., 2018, 2015; Faria et al., 2009) and there is no information at all for haddock larvae.

In Europe, the largest stocks of haddock are located in the Barents Sea (Northeast Atlantic stocks) (Bergstad et al., 1987) and in the North Sea (Daan et al., 1990). Haddock is demersal; juvenile habitat is associated with the continental shelf/slope and coastal areas (Albert, 1994). In the North Sea, this species undertakes seasonal migrations between the spawning grounds located north-northwest and the more southern feeding areas (Daan et al., 1990; Thompson, 1927). The general circulation pattern of the North Sea results in a south-southeastward drift of haddock larvae, from the spawning areas toward the Skagerrak and the Norwegian trench (Albert, 1994; Heath and Gallego, 1998). Behavioral observations of haddock larvae have focused mainly on feeding (Petrik et al., 2009) and vertical migration during the dispersal phase (Werner et al., 1993). However, little is known about the swimming behavior of haddock larvae at sea, and there is currently no information on whether they perform active and directional swimming or drift

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passively with the currents. Research on these aspects of haddock larval behavior is needed, as they would make an important contribution to our ability to model retention and dispersal of this species during the early-life stages.

Many late larval stage fish perform oriented swimming in response to/guided by a multiplicity of environmental cues. The larvae of coral reef and Mediterranean fish species use cues such as the sun (Faillietaz et al., 2015; Mouritsen et al., 2013), sound of the reef (Leis et al., 2003; Simpson et al., 2004), polarized light (Berenshtein et al., 2014), and odors (Foretich et al., 2017; Paris et al., 2013) to orient. However, some of these cues might be patchy or unavailable in offshore and/or in deep waters. The only ubiquitous, steady, and directional cue, available at all times, is the Earth's magnetic field. The larvae of some coral reef fish have a magnetic field-based compass mechanism (Bottesch et al., 2016; O'Connor and Muheim, 2017) that they might use to reduce dispersal (Bottesch et al., 2016). Similar abilities were reported in post-larval glass eels, which use a magnetic compass linked to an endogenous tidal clock to guide their swimming and orientation (Cresci et al., 2017). However, whether high-latitude fish such as haddock have magnetic orientation abilities at the larval stage is not known.

In this work, we explored the possibility that the pelagic larvae of haddock from the North Sea orient using the Earth's magnetic field. To test this hypothesis, we used a transparent drifting *in situ* chamber (DISC, Paris et al., 2008) to observe the orientation of haddock larvae *in situ*. We also tested the orientation of haddock larvae while swimming in DISC when inside a magnetic laboratory facility (MagLab) in which the magnetic field could be manipulated in three dimensions.

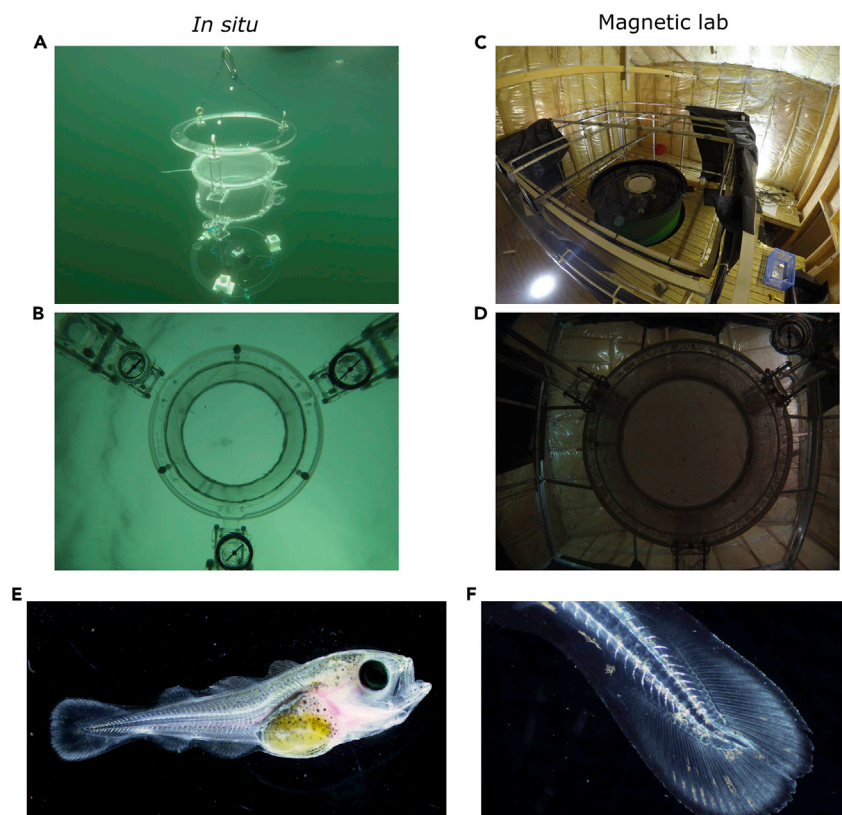
## RESULTS

When tested *in situ*, 91% of larvae (54 of the 59 tested) oriented significantly (Rayleigh test of uniformity applied to the track of each larva (Rayleigh's  $p < 0.05$ ; Figure S1.3) swimming in the DISC at sea (Figures 1A and 1B). In the MagLab (Figures 1C and 1D), 99% of the larvae (101 of the 102 larvae tested) displayed significant orientation. The haddock larvae that oriented displayed the same mean orientation direction (Figure S1.4) *in situ* and in the MagLab (Figure 2). Larvae significantly oriented toward the northwest *in situ* ( $N = 54$ ; mean angle =  $313^\circ$ , magnetic declination =  $+1.1^\circ$ ,  $r = 0.26$ ,  $p = 0.03$ ; Figure 2) and oriented toward the same direction, the magnetic northwest, in the MagLab ( $N = 101$ ; mean angle =  $318^\circ$ , magnetic declination =  $+1.1^\circ$ ,  $r = 0.34$ ,  $p = 0.00001$ ; Figure 2). The mean directions of the larvae swimming *in situ* and in laboratory conditions did not differ statistically (Mardia-Watson-Wheeler test  $p = 0.49$ ).

## DISCUSSION

Haddock larvae exhibited significant orientation direction when swimming *in situ*, and the experiments conducted in the MagLab revealed that this is based on a magnetic compass mechanism. These results are consistent with earlier studies showing that fish larvae and adults of multiple species use the Earth's magnetic field to guide their movement. For example, salmon use magnetic cues, imprinted on first contact with saltwater, to find their home estuary later in life (Lohmann et al., 2008; Putman et al., 2013). The magnetic compass of sockeye salmon smolts (*Oncorhynchus nerka*) depends on the availability of celestial cues (Quinn, 1980), indicating that these orientation mechanisms can be based on a complex combination of multiple cues. Magnetic orientation was also reported in adult European eel (*Anguilla anguilla*), which are able to detect spatial displacement and reorient using the magnetic field (Durif et al., 2013). Similar abilities were documented in post-larval glass eel, which use a compass mechanism linked to the rhythm of the tide (Cresci et al., 2017). The pelagic larvae of the tropical reef fish, the four line cardinalfish (*Ostorhinchus doederleinii*), use a magnetic compass mechanism to orient against the direction of the current that would otherwise transport them far from the reef (Bottesch et al., 2016). For haddock larvae, the magnetic compass observed in this study could possibly serve a similar function, but on a larger spatial scale.

Haddock larvae develop caudal, anal, and dorsal fin rays and grow large pectoral fins, when they are 8–9 mm in length (Auditore et al., 1994) (Figures 1E and 1F), which greatly improves their swimming ability and maneuverability. Based on the locations at which larvae of different ages were distributed, it was estimated that they might swim at speeds ranging from 0.65 to 1 cm s<sup>-1</sup> (Lough and Bolz, 2006). These swimming speeds, coupled with the orientation abilities observed here, could play a significant role in the dispersal and retention of haddock larvae in the North Sea. The inflow of saline Atlantic water from the north is the main factor driving the overall circulation pattern of the North Sea (Sundby et al., 2017). Atlantic water enters the region through two large branches. One shallower current flows along the eastern

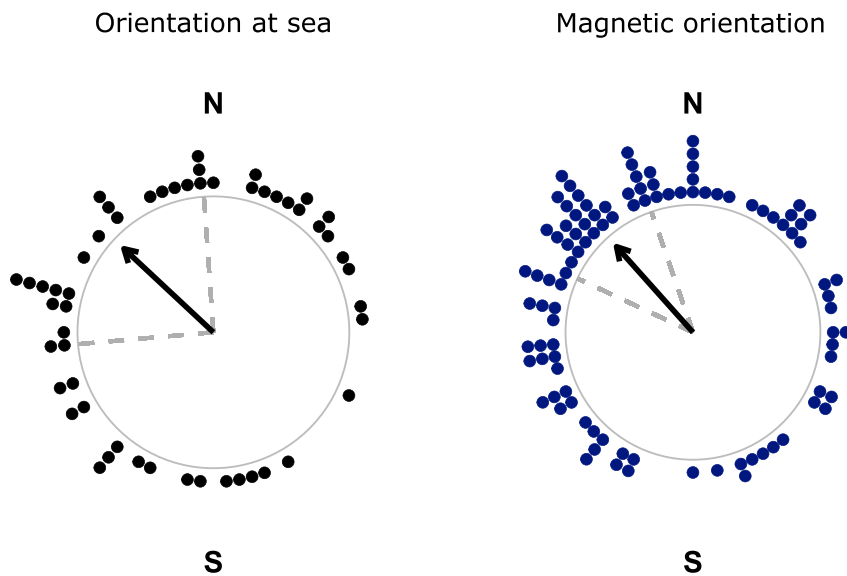


**Figure 1. DISC (Drifting In Situ Chamber), Magnetic Laboratory (MagLab), and Haddock Larvae (*Melanogrammus aeglefinus*) Used in the Experiments**

(A) Photograph of the DISC drifting at sea. The main underwater unit is composed of the chamber, the acrylic frame, the camera, and sets of sensors. In this study the arena has a diameter of 20 cm and is placed 30 cm above a GOPRO camera. (B) Example of an image from the upward-looking camera placed underneath the behavioral chamber of the DISC. (C) View of the electric coils setup in the MagLab designed to modify the magnetic field in three dimensions. A tank filled with seawater is present at the center of the coils. The same device used *in situ* (DISC) is placed at the center of the tank. (D) Example of an image from the upward-looking camera placed underneath the behavioral chamber of the DISC in the MagLab. (E) Photograph of larval haddock at 38 days post hatch (dph). (F) Zoomed-in view of the caudal fin of the larva at 38 dph.

Shetlands, and the second deeper current enters the North Sea at the western boundary of the Norwegian trench (Sundby et al., 2017). This water mass defines the northern sub-region of the North Sea, where there is the highest diversity of fish species (Heessen et al., 2015). These areas also host the main spawning grounds of the North Sea haddock, located near the continental slope of North East Scotland and the Orkney and Shetland Isles (Daan et al., 1990; Heath and Gallego, 1998). In this context, haddock are hypothesized to be separated into two main sub-populations within the northern part of North Sea, a north-western and a northeastern one (Wright et al., 2011).

From these areas, the general circulation of the North Sea flows mainly southward with a branch expanding southeast toward the Skagerrak and the Norwegian deep (Albert, 1994; Heath and Gallego, 1998; Turrell, 1992). These currents transport eggs, larvae, and juvenile haddock southeastward toward the Norwegian trench and the Skagerrak area (Munk et al., 1999; Sundby et al., 2017). As the larvae oriented toward the magnetic northwest, it is possible that the magnetic orientation direction observed in this study serves as an innate mechanism that limits the dispersal of haddock larvae toward the southeast (as would be the case if they drifted passively with the current). This orientation behavior could also play an important role at the western boundaries of the Norwegian trench, where a spawning area of North Sea haddock is located (Munk et al., 1999). Here, the circulation differs from the rest of the North Sea as the current flows



**Figure 2. Orientation of the Haddock Larvae (*Melanogrammus aeglefinus*) at Sea and in the Magnetic Laboratory (MagLab)**

Orientation is presented with respect to the magnetic north (N) and south (S). Each black point corresponds to the mean bearing of one haddock larva *in situ* (averaged over 600 data points from the video tracks, Figure S1) (N = 54). Each navy blue data point is the mean bearing of one haddock larva in the magnetic laboratory (N = 101). During the experiments, the magnetic north in the laboratory was rotated for each larva (i.e., the magnetic north in the laboratory had a different direction for each of the blue data points). This figure displays the mean bearings of the larvae that showed an individual preferred orientation. The black arrow points toward the mean angle of all the individual bearings (mean bearing *in situ* = 313°,  $p = 0.03$ ; mean bearing in the MagLab = 319°,  $p = 0.00001$ ). Dashed gray lines are the 95% confidence intervals around the mean.

to the north (Sundby et al., 2017) in the form a narrow jet of less saline water coming from the Baltic, known as the Norwegian Coastal Current (Mork, 1981). This current flows along the western coast of Norway and exits the basin following the Norwegian coast up to the Barents Sea. Magnetic orientation to the northwest could help haddock larvae to exit the western boundary of the Norwegian trench, where larvae would drift north and possibly disperse out of the basin. This possibility is further supported by simulations of larval dispersal showing that orientation behavior significantly affects dispersal at the boundaries of the Norwegian current (Fiksen et al., 2007; Vikebø et al., 2007).

Although haddock undertake migrations from the feeding to the spawning grounds, the distance that they cover during their life cycle is still fairly limited compared with other pelagic fish (e.g., herring) (Daan et al., 1990). Thus, behavioral mechanisms such as magnetic-based orientation during the early life stages might play a role in the distribution of this species, as this would help retention in the northern area of the North Sea where this species is most abundant (Albert, 1994). However, the orientation direction of haddock larvae could vary depending on the stocks and local populations. It is possible that populations from different areas of the North Atlantic display different magnetic orientation directions. Indeed, haddock may adapt to local oceanographic conditions, as orientation to the northwest could be beneficial in the North Sea, but this might not be the case for haddock from other regions. These scenarios should be explored experimentally in future work by testing the orientation behavior of haddock from different areas and stocks. Moreover, the role of orientation behavior during the dispersal phase should also be tested using biophysical modeling that incorporates the swimming and orientation behavior.

As adult haddock in the Norwegian Deep and other areas of the North Sea undertake spawning migrations (Albert, 1994), a magnetic-compass-based orientation could be important in the journey toward the spawning areas and back. Whether haddock conserve a compass-based magnetic orientation from the larval stage through adulthood is unknown. Future work will investigate whether adult haddock display the same abilities as larvae.

## Limitations of the Study

In the present study, the orientation behavior was not compared between different populations of haddock. The behavior described here might vary according to the different populations and geographical areas. Furthermore, we used the age of the larvae and the temperature at which they were reared as an indirect indicator of larval growth. However, we did not record larval length, which is a more direct measure of larval growth.

## METHODS

All methods can be found in the accompanying [Transparent Methods supplemental file](#).

## SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.isci.2019.09.001>.

## ACKNOWLEDGMENTS

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## AUTHOR CONTRIBUTIONS

A.C. designed the study; collected, analyzed, and interpreted the data; and wrote the paper; C.B.P. designed the study; collected, analyzed, and interpreted the data; wrote the paper; and funded the research; M.A.F. analyzed and interpreted the data; C.M.D. designed the study, collected and interpreted the data; S.D.S. collected and analyzed the data; C.J.E.O. collected and analyzed the data; F.B.V. interpreted the data, wrote the paper, and funded the research; A.B.S. designed the study, collected and interpreted the data, wrote the paper, and funded the research; H.I.B. designed the study, collected and interpreted the data, wrote the paper, and funded the research.

## DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

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**ISCI, Volume 19**

## **Supplemental Information**

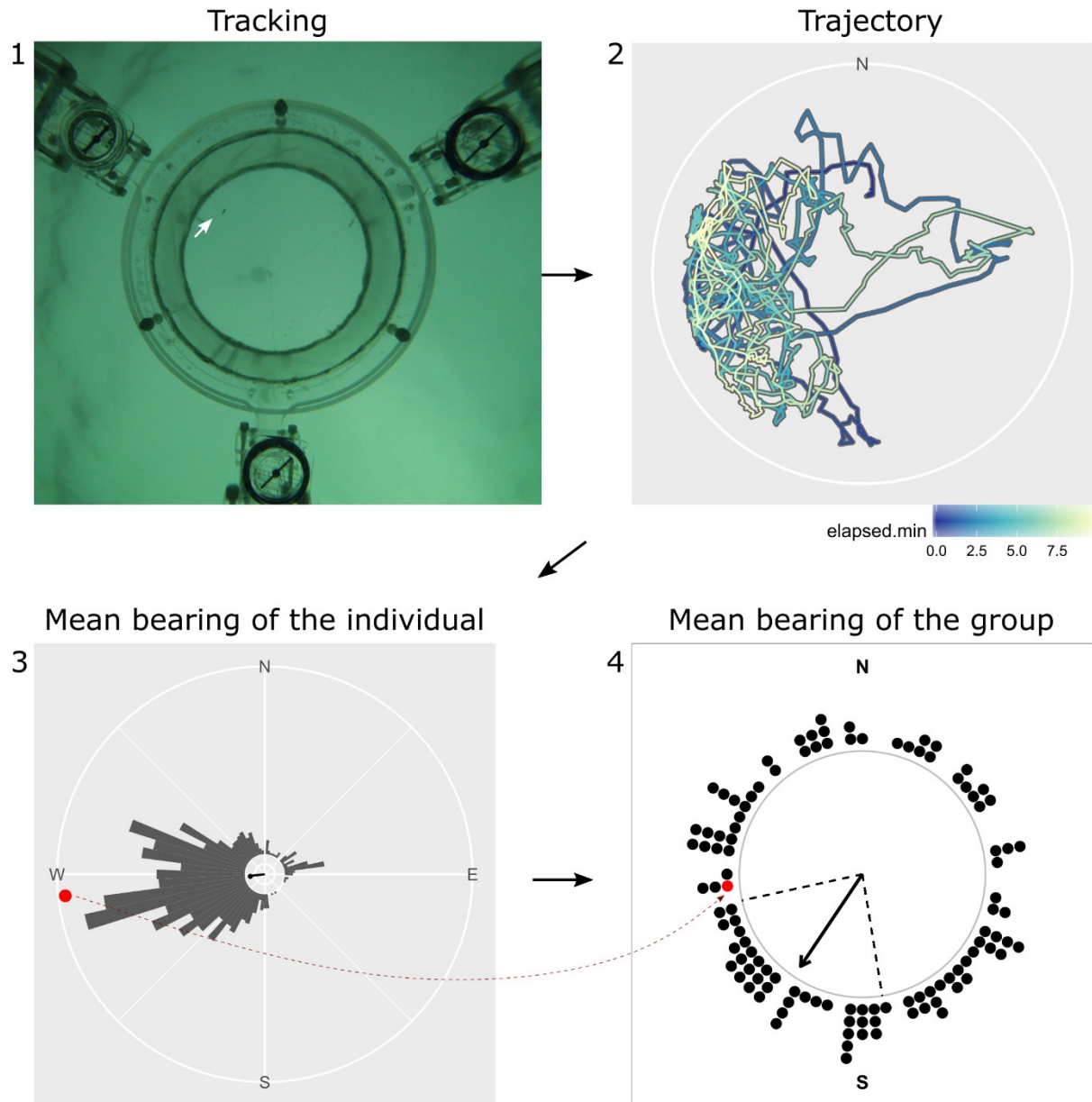
**Atlantic Haddock (*Melanogrammus aeglefinus*)**

**Larvae Have a Magnetic Compass**

**that Guides Their Orientation**

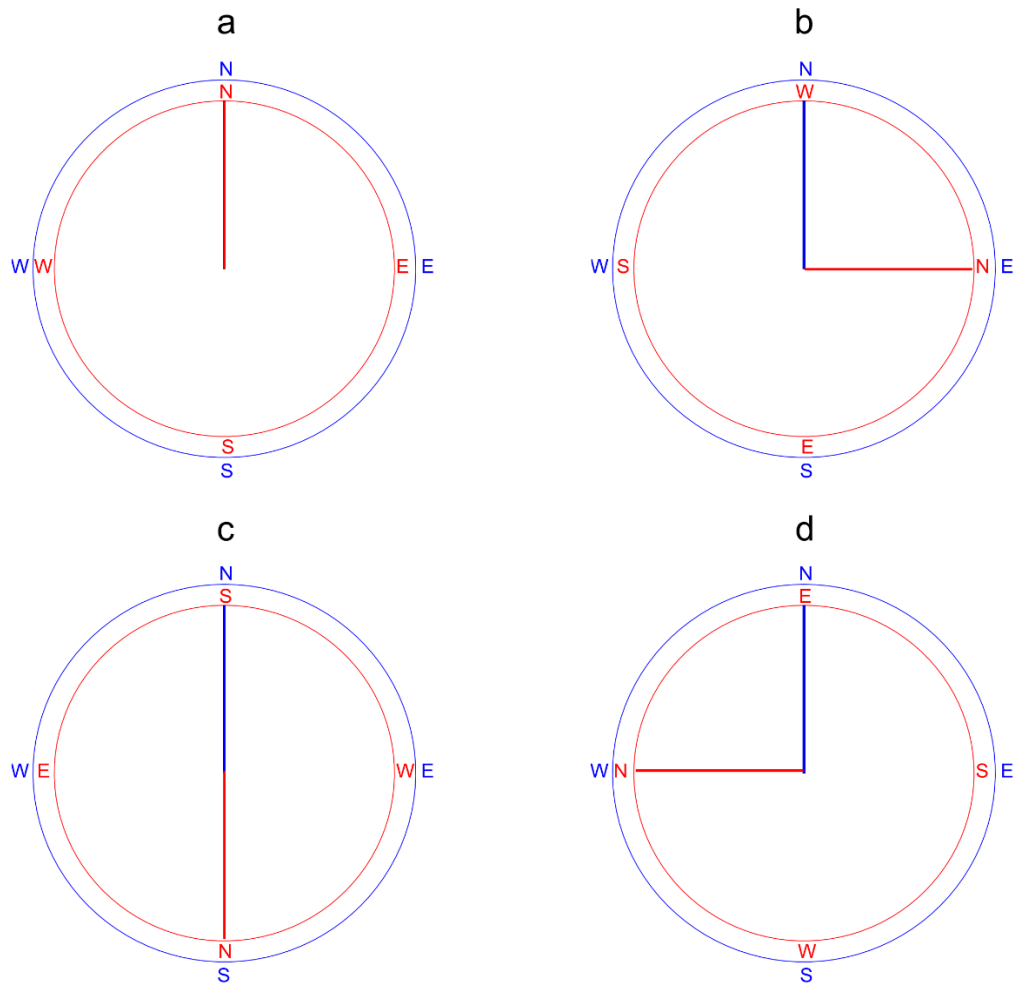
**Alessandro Cresci, Claire B. Paris, Matthew A. Foretich, Caroline M. Durif, Steven D. Shema, CJ E. O'Brien, Frode B. Vikebø, Anne Berit Skiftesvik, and Howard I. Browman**

## SUPPLEMENTAL INFORMATION

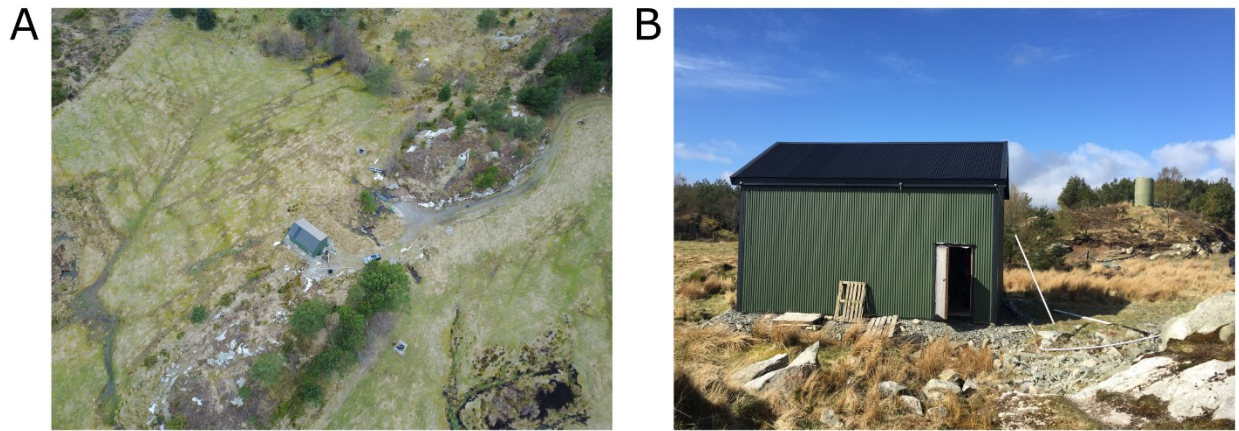


**Figure S1. Description of the analysis of the data collected with the DISC, Related to Figure 1 and Figure 2.** **1:** The first step is to collect data on the position of the larvae in the DISC using a tracking procedure conducted on the videos recorded *in situ* during the deployments. The position of each larva is tracked every second for 10 minutes (i.e. 600 data points are collected per each fish tested in the DISC). The photo shows an example of the view of a haddock larva (highlighted by a white arrow) swimming in the behavioral chamber of the DISC. **2:** The trajectory of the larva is calculated from the datapoints collected through the video tracking. **3:** The angle of each of the 600 data points with respect to the magnetic North and the center of the chamber is considered as a bearing. Because the DISC is allowed to rotate, bearings are corrected using the digital compass that records the difference between the orientation of the camera and the magnetic North. The mean orientation of the larva is assessed by applying Rayleigh's test of

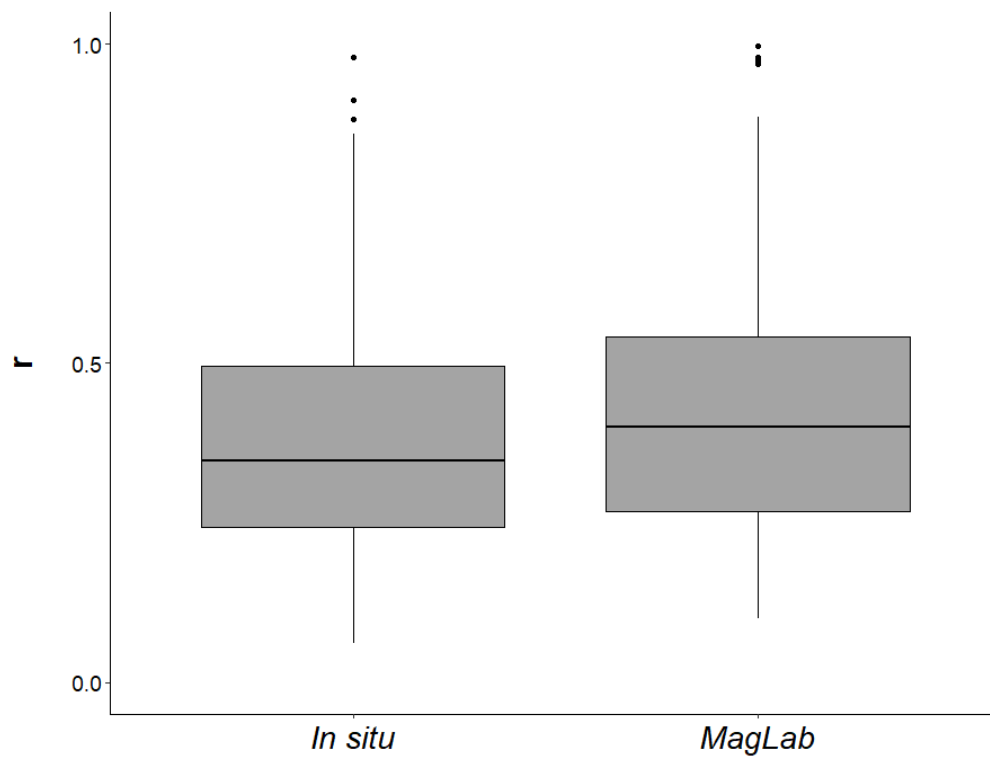
uniformity on the 600 bearings. If the outcome of the statistical test is significant ( $p < 0.05$ ), the mean bearing (red circle in this example) is considered as the preferred orientation direction of the larva. **4:** The last step of the analysis is performed on all of the preferred orientation directions of the larvae from the same experimental group (i.e. all the larvae tested *in situ*). The mean orientation directions of the larvae are grouped and the Rayleigh's test is applied. Through this step we assess whether the larvae had the tendency to orient towards a common direction. In this panel of the figure the red circle corresponds to the mean orientation of the larva used as an example in the previous panel # 3. In this hypothetical example, larvae had the tendency to orient SW (direction indicated by the black arrow, with the dashed lines indicating the 95% confidence intervals).



**Figure S2. Schematic diagram of the magnetic protocol, Related to Figure 1C, 1D.** Blue N, E, S, W represent the Earth's magnetic cardinal points. Red N, E, S, W correspond to the magnetic cardinal points in the testing tank. The red line highlights the orientation of the magnetic North and the blue line the orientation of the Earth's magnetic North. Each larva was observed in one of these four magnetic conditions. The orientation was then assessed with respect the North in the tank (red North).



**Figure S3. Photos of the MagLab, Related to Figure 1C.** **A.** Aerial drone photo of the MagLab taken using a DJI Mavic Pro. **B.** Side view of the Maglab.



**Figure S4, Related to Figure 2.  $r$  values.** Boxplot of the  $r$  values from the Rayleigh's test of uniformity applied on the individual tracks of the larvae tested in situ and in the MagLab.

**Table S1, Related to Figure 2.** Date and time of the *in situ* deployments and the age of the haddock larvae (*Melanogrammus aeglefinus*). A total of 59 larvae were tracked.

Date	Time start	Time stop	N fish tracked	Age (dph)
2015-04-23	16:54:00	17:10:00	2	31
2015-04-23	17:13:00	17:29:00	2	31
2015-04-23	17:31:00	17:47:00	1	31
2015-04-23	17:50:00	18:06:00	2	31
2015-04-23	18:08:00	18:24:00	2	31
2015-04-23	18:27:00	18:43:00	1	31
2015-04-23	18:46:00	19:02:00	1	31
2015-04-23	19:04:00	19:20:00	2	31
2015-04-23	19:23:00	19:39:00	1	31
2015-04-23	19:41:00	19:57:00	1	31
2015-04-27	10:24:00	10:41:00	2	35
2015-04-27	10:43:00	10:59:00	2	35
2015-04-27	11:01:00	11:18:00	1	35
2015-04-27	11:22:00	11:38:00	2	35
2015-04-27	11:41:00	11:57:00	2	35
2015-04-27	11:59:00	12:17:00	1	35
2015-04-27	12:19:00	12:34:00	2	35
2015-04-27	12:36:00	12:52:00	2	35
2015-04-27	12:55:00	13:11:00	1	35
2015-04-27	13:14:00	13:30:00	3	35
2015-04-28	16:28:16	16:43:51	2	36
2015-04-28	16:45:23	17:01:04	2	36
2015-04-28	17:02:33	17:19:50	2	36
2015-04-28	17:21:58	17:38:21	2	36
2015-04-28	17:40:30	17:56:00	2	36
2015-04-28	17:58:24	18:14:24	1	36
2015-04-28	18:16:49	18:32:30	1	36
2015-04-28	18:34:17	18:50:14	2	36
2015-04-28	18:51:44	19:07:47	2	36
2015-04-28	19:10:17	19:26:04	2	36
2015-05-01	11:32:00	11:47:00	2	39
2015-05-01	11:50:00	12:05:00	2	39
2015-05-01	12:09:00	12:24:00	2	39
2015-05-01	12:32:00	12:47:00	1	39
2015-05-01	12:51:00	13:06:00	1	39

**Table S2, Related to Figure 2.** Date and time of the tests in the MagLab, and age of the haddock larvae (*Melanogrammus aeglefinus*). The rotation of the magnetic north during each test is shown (i.e. mf.south = magnetic north in the lab rotated towards the earth's magnetic south). A total of 102 larvae were tracked.

Date	Time start	Time stop	N fish tracked	Age (dph)	Rotation magnetic North
2015-04-24	15:59:00	16:14:00	2	32	mf.north
2015-04-24	16:16:00	16:31:00	2	32	mf.south
2015-04-24	16:35:00	16:05:00	2	32	mf.east
2015-04-24	16:52:00	17:07:00	2	32	mf.west
2015-04-24	17:09:00	17:24:00	2	32	mf.north
2015-04-24	17:26:00	17:41:00	2	32	mf.south
2015-04-24	17:44:00	17:59:00	2	32	mf.east
2015-04-24	18:02:00	18:17:00	2	32	mf.west
2015-04-24	18:19:00	18:34:00	2	32	mf.north
2015-04-24	18:37:00	18:52:00	2	32	mf.south
2015-04-24	18:55:00	19:10:00	2	32	mf.east
2015-04-24	19:12:00	19:27:00	2	32	mf.west
2015-04-25	15:57:00	16:12:00	2	33	mf.north
2015-04-25	16:15:00	16:30:00	2	33	mf.south
2015-04-25	16:32:00	16:47:00	2	33	mf.east
2015-04-25	16:49:00	17:04:00	2	33	mf.west
2015-04-25	17:06:00	17:21:00	2	33	mf.north
2015-04-25	17:24:00	17:39:00	2	33	mf.south
2015-04-25	17:42:00	17:57:00	2	33	mf.east
2015-04-25	17:59:00	18:14:00	2	33	mf.west
2015-04-25	18:15:00	18:30:00	2	33	mf.north
2015-04-25	18:32:00	18:47:00	2	33	mf.south
2015-04-25	18:49:00	19:04:00	2	33	mf.east
2015-04-25	19:07:00	19:22:00	2	33	mf.west
2015-04-25	19:24:00	19:39:00	2	33	mf.north
2015-04-25	19:41:00	19:56:00	2	33	mf.south
2015-04-29	15:32:00	15:47:00	2	37	mf.east
2015-04-29	15:49:00	16:04:00	2	37	mf.west
2015-04-29	16:06:00	16:21:00	2	37	mf.north
2015-04-29	16:23:00	16:38:00	2	37	mf.south
2015-04-29	16:40:00	16:55:00	2	37	mf.east
2015-04-29	16:57:00	17:12:00	2	37	mf.west
2015-04-29	17:14:00	17:29:00	2	37	mf.north
2015-04-29	17:32:00	17:47:00	2	37	mf.south
2015-04-29	17:50:00	18:05:00	2	37	mf.east
2015-04-29	18:07:00	18:22:00	2	37	mf.west
2015-04-29	18:24:00	18:39:00	2	37	mf.north
2015-04-29	18:41:00	18:56:00	2	37	mf.south

2015-04-29	18:58:00	19:13:00	2	37	mf.east
2015-04-30	14:28:00	14:43:00	2	38	mf.west
2015-04-30	14:45:00	15:00:00	2	38	mf.north
2015-04-30	15:01:00	15:16:00	2	38	mf.south
2015-04-30	15:18:00	15:33:00	2	38	mf.east
2015-04-30	15:34:00	15:49:00	2	38	mf.west
2015-04-30	15:51:00	16:06:00	2	38	mf.north
2015-04-30	16:08:00	16:23:00	2	38	mf.south
2015-04-30	16:26:00	16:41:00	2	38	mf.east
2015-04-30	16:42:00	16:57:00	2	38	mf.west
2015-04-30	16:59:00	17:14:00	2	38	mf.north
2015-04-30	17:16:00	17:31:00	2	38	mf.south
2015-04-30	17:33:00	17:48:00	2	38	mf.east

**Table S3, Related to Figure 2.** Mean direction and r values from the Rayleigh's test applied on the video track of each haddock larva (*Melanogrammus aeglefinus*). The experimental group is also reported (*in situ*/Maglab).

## Transparent Methods

### *Larval rearing and collection*

Haddock broodstock were collected locally from the waters near Austevoll, Norway. Five 100 L tanks were inoculated with 100 larvae/liter. The inflow was maintained at 4 liter/minute and tanks were kept in 24h light under 2 x 25w, 12 V halogen lamps. The larvae were reared in green water (Nannochloropsis, Reed Mariculture) at a temperature of 11-12°C and salinity of ca. 35 PSU. Larvae were fed first on a diet of rotifers (*Brachionus sp.*), and then on copepods (primarily *Acartia sp.*). Larvae with full guts were removed from the rearing tanks at least 12 hours prior to be deployed *in situ* and were placed into 120 mL cups, with two larvae per cup. Zooplankton was added to each cup to provide continuous food. The cups were placed in 20 L of 12°C water that was then immersed in a 6–7°C water bath 12 h before the tests to acclimate the larvae to the local seawater temperatures at 4 m depth in the deployment area.

### *Experimental device and deployments in situ*

To collect data on orientation and swimming behavior at sea we video recorded haddock larvae while swimming in a transparent drifting circular arena (Drifting In Situ Chamber, DISC, Paris et al., 2013, 2008). We used larvae of 31-39 days post hatch (dph) larvae - which had fully formed fin rays (Fig. 1F) - for the *in situ* tests (Fig. 1E). All tests were conducted in April-May 2015 in the coastal areas of a Norwegian fjord (Bjørnafjorden, Northeast of Austevoll, 60.09 N, 5.28 E).

The DISC is a drifting circular arena with an acrylic structure and a semi-open transparent circular chamber 20 cm wide and 10 cm deep. The lower part of the DISC is attached to a drogue, which allows the whole system to drift with the current (Paris et al., 2013). The DISC is equipped with a GOPRO camera, three analog compasses and a custom Arduino digital compass. When the DISC is placed in the water, the circular arena drifts at a depth of ca. 4 m. Because of the DISC setup, the behavioral chamber is between the sea surface and the camera. This allows the light contrast to improve the visibility of the larvae in the chamber, which is important for the following data analysis of the videos. For each deployment, we held the DISC semi-submerged along the side of the boat and placed two haddock larvae into the arena.

Afterwards, the DISC was released and allowed to drift for 15 minutes. We considered the first 5 minutes of each deployment as an acclimation period and we analyzed the larval swimming behavior during the last 10 minutes (Paris et al., 2013). All of the videos were processed using the DISCR tracking procedure, utilizing R and a graphical user interface provided by imageJ software (Irisson et al., 2009, 2015). The open-source code utilized (GNU General Public License v3.0) is available at the web page (<https://github.com/jiho/discr>).

We tracked the position of each fish, every second, for a 10 minute period of each deployment (600 data points per each larva). See Fig. S1 for a detailed diagram of all of the steps in the analysis. We consider each position of the fish with respect to the center of the arena (in degrees) as a single data point, which we call bearing (in literature, the term “bearing” has been used to describe directed movement; here, we use it to describe spatial preference). Afterwards, we corrected the bearings with respect to the magnetic north using the digital compass. If the frequency distribution of the 600 bearings was significantly different from random (Rayleigh’s  $P < 0.05$ ), we considered it as evidence of orientation, and we used the mean individual bearing as the orientation direction of the larva. The null hypothesis of the Rayleigh’s test is uniformity of the distribution of the bearings. The alternative hypothesis is a unimodal or a Von Mises distribution (which is narrower than the unimodal) with a mean angle, representing the mean direction of the larva. This test is particularly recommended for  $>30$  data points (here it is 600 per fish) (Batschelet, 1981).

The next step of the analysis was to evaluate whether the larvae of each experimental group (larvae tested *in situ* vs. those tested in the MagLab) were swimming towards a common direction (whether they had common orientation direction; Fig S1.4). To explore that, we used Rayleigh’s test of uniformity applied to all of the mean individual bearings of all of the larvae from each of the experimental groups as data points ( $N = 54$  *in situ*;  $N = 101$  in the MagLab). If Rayleigh’s  $P$  was  $< 0.05$  we considered the group as showing a common orientation and we interpreted the mean as the overall common direction of the group.

#### *Experiments in the magnetic laboratory*

The experiments in the MagLab followed the same protocol as described in Cresci et al. 2017 (Cresci et al., 2017). The MagLab is designed to study the magnetic orientation of aquatic animals. It is equipped with a triaxial electric coil system (Fig. 1C), with a design described by Merritt et al. (Merritt et al., 1983), and connected to a power supply (max. 3 A). At the center of the coils, there is a black circular tank made of fiberglass (diameter, 1.40 m; height, 0.90 m; see Fig. 1C) filled with seawater, which is pumped from the sea 300 m away. The building (see fig. S3A; S3B) is constructed of nonmagnetic material and is far from any source of magnetic interference (163 m from the nearest electrical disturbance and 365 m from the closest building; Fig. S3B).

For the tests in the MagLab, we used the DISC as a behavioral chamber, submerged in the circular dark tank (see Fig. 1C). The chamber was the same as the one used for the tests *in situ*. The top of the chamber was covered with opaque white plastic, which diffused light uniformly in the chamber (Fig. 1D). Light intensity in the tank was low (around 0 lum/ft<sup>2</sup> as measured by a HOBO light sensor on the bottom plate of the DISC frame). The DISC was equipped with an analog compass attached to the acrylic poles of the DISC frame and placed below the circular arena. This positioning eliminates the possibility that the compass would be a visual reference for the larvae.

The laboratory is equipped with two nested electric coil systems described in Durif et al. (2013). One was used to cancel out the horizontal component of the ambient field. With the second coil system, we were able to generate a magnetic field with the same total intensity as the ambient field (48.8 to 50  $\mu$ T) and to reorient the magnetic north. The intensity and inclination inside the coil were set to match the ambient field (48.8 to 50  $\mu$ T and 73°, with a deviation of  $<1^\circ$ ).

For these tests, we used larvae ranging between 32 and 38 dph (Table S2). Each larva was observed for 15 min, with the first 5 min considered as an acclimation period (as for the tests *in situ*) (Cresci et al., 2017; Paris et al., 2013), under one of the four simulated magnetic field conditions, with the magnetic north reoriented to the Earth’s east, south, west, or north (see Fig. S2). Each larva experienced only one of these four magnetic conditions. Using this approach, we eliminated any nonmagnetic bias that could have influenced the orientation response of the animals. Moreover, the MagLab is designed to cancel out

all the possible external cues that animals could use for orientation except for the magnetic field, as the animals are not exposed to water flows, odor plumes, sunlight or any celestial cues. All tests were conducted during daytime under artificial light.

The orientation of the larvae was determined through the analysis of the GOPRO images following the same process described in the previous section (see also Fig. S1). However, the magnetic north had a different orientation in the laboratory during each test, and the position of the larva was corrected with respect of the magnetic north in the lab (Fig. S2, red North = 0°) using the digital compass.

## Ethics statement

The Austevoll Research Station has the following permits - issued by the Norwegian Directorate of Fisheries - catch and maintain Atlantic haddock: H-AV 77, H-AV 78 and H-AV 79. The Austevoll Research Station is also a certified Research Animal Facility for all developmental stages of fish under Code 93 from the National Institutional Animal Care and Use Committee (IACUC), NARA. We did not need specific approval for these experiments because they are non-intrusive behavioral observations and larvae were sacrificed using an approved humane endpoint process after the trials.

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