

ANIMAL MIGRATION

Glass eels (*Anguilla anguilla*) have a magnetic compass linked to the tidal cycle

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The European eel (*Anguilla anguilla*) has one of the longest migrations in the animal kingdom. It crosses the Atlantic Ocean twice during its life history, migrating between the spawning area in the Sargasso Sea and Europe, where it is widely distributed. The leptocephalus larvae drift with the Gulf Stream and other currents for more than a year and metamorphose into glass eels when they arrive on the continental shelf and move toward coastal areas. The mechanisms underlying glass eel orientation toward the coast and into freshwater systems are poorly known. However, anguillid eels, including the glass eel life stage, have a geomagnetic sense, suggesting the possibility that they use Earth's magnetic field to orient toward the coast. To test this hypothesis, we used a unique combination of laboratory tests and in situ behavioral observations conducted in a drifting circular arena. Most (98%) of the glass eels tested in the sea exhibited a preferred orientation that was related to the tidal cycle. Seventy-one percent of the same eels showed the same orientation during ebb tide when tested in the laboratory under a manipulated simulated magnetic field in the absence of any other cue. These results demonstrate that glass eels use a magnetic compass for orientation and suggest that this magnetic orientation system is linked to a circatidal rhythm.

INTRODUCTION

The European eel (*Anguilla anguilla*) spawns at sea but spends most of its life in freshwater or coastal habitats throughout Europe and from Northern Africa to the North Cape in Norway. This critically endangered species [International Union for Conservation of Nature (IUCN)] is an important commercial resource, and its population has decreased markedly since the 1980s (1–3). European Union member states are required to establish management plans to restore its population, and this has stimulated research on both conservation and management of eels (4). Stocking of postlarval glass eels and pigmented juvenile eels (elvers) to locations where the population is most depleted is a widespread management practice. However, a deeper knowledge about the ecological consequences of eel releases is needed to improve the reproductive success of the transferred individuals (5). Research about their orientation mechanisms is also important to assess how the translocation of restocked glass eels affects the way that they integrate spatial cues when entering coastal and inland habitats—cues that they may use when returning to the spawning areas later in life.

The European eel migrates across the Atlantic Ocean twice during its life. Silver eels leave freshwater and coastal habitats from areas across their distribution range and migrate to the spawning area in the Sargasso Sea (6). Eggs released at the spawning area hatch into leptocephalus larvae that drift with the currents. During this pelagic larval phase, leptocephali are transported toward the European continent (7–10), and as they approach the continental shelf, they metamorphose into the postlarval form, the glass eel (11, 12). Glass eels migrate to coastal and freshwater habitats (8, 13), where they recruit as elvers. They then spend the growth phase of their life cycle as yel-

low eels (most often 5 to 20 years). Finally, toward the end of their life cycle, they transform into silver eels.

Eel leptocephali might drift passively across the Atlantic with the currents. However, it is also possible that at some point during the later stages of the journey, they swim in an oriented manner (8, 10, 14). The leptocephali are transported from the Sargasso Sea to Europe via two main routes: one is northeastward, and one is a more direct route toward the east (9). According to a length-frequency analysis of the large database of leptocephali sampled at sea, this pelagic larval phase may last from 17 to 28 months (9). During the early larval pelagic phase, leptocephali migrate vertically in the upper 50 to 300 m (15) and between 300 and 600 m as they approach the continental shelf (11). Thus, considering the vertical migration of leptocephali, and the variability of the current velocity with depth, passive drifting alone seems insufficient to explain how the larvae complete their long migration. Furthermore, a coupled biophysical model predicted that setting particles to swim along a preferred bearing increased their survival and recruitment to the continental shelf compared to those modeled as passive drifters (16). Later in their life cycle, leptocephali metamorphose into the postlarval glass eel stage as they move onto the continental shelf in search of the outflows of freshwater streams.

The mechanisms and environmental cues underlying the orientation of glass eels in pelagic and coastal areas are poorly known. Ichthyoplankton surveys and laboratory-based experiments indicate that glass eels are attracted by terrestrial odor cues, low salinity, and colder temperature (17–22). However, these cues provide directional information in the form of gradients that are highly variable because of weather conditions, glacier melt, and marine circulation patterns (23). Thus, on their own, these cues are insufficient to explain the successful orientation of glass eels to freshwater outlets.

Earth's magnetic field represents a stationary frame of reference for animal navigation (24, 25), providing a directional cue that would allow any marine animal that could perceive it to orient in the absence of any other environmental cue (26–31). Animals of numerous taxa, ranging from insects to birds and mammals, can perceive Earth's magnetic field (26). In the marine environment, crustaceans

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such as spiny lobsters (*Panulirus argus*) are able to detect magnetic variations in the latitude and longitude and orient using magnetic maps (27). Similarly, Pacific salmon (*Oncorhynchus nerka*) and loggerhead sea turtles (*Caretta caretta*) use magnetic orientation for long oceanic migrations and homing to natal areas (28–30).

Laboratory-based studies demonstrated that eels are also able to detect magnetic fields at different life stages. As silver eels, they orient magnetically using a magnetic compass system (31, 32). Additionally, an American silver eel tracked by a pop-up satellite tag followed a direct, quasi-straight route from the Canadian coast to the Sargasso Sea (33). This ocean transect is characterized by weak horizontal thermohaline gradients that would not provide a consistent and reliable orientation cue, implying the possible involvement of magnetic orientation (33). Eels can also orient with magnetic fields at the yellow eel stage. Yellow eels of *Anguilla rostrata* orient to the northeast when placed in an octagonal chamber in the presence of Earth's magnetic field (34). Similarly, female yellow eels (*A. anguilla*) in a freshwater pond preferred shelters oriented along the south-southwest–north-northeast axis during the fall, suggesting a seasonally dependent magnetic orientation (35). Additionally, European yellow eels (*A. anguilla*) can follow 90° directional shifts of the magnetic field (36). Eels may be able to detect magnetic fields very early in their life history. Glass eels of *Anguilla ja-*

ponica slow down their heart rate after conditioning with imposed weak magnetic fields (37). Elvers of *A. rostrata* display orienting behavior related to the direction and intensity of the electric field, with higher turning frequency toward the anode (38, 39). However, the link between turning directions of elvers and the magnetic field has not been demonstrated (38). Moreover, none of the experiments carried out on the orientation of early life stages of eels have been able to disentangle the effect of the magnetic field and a potential effect of the electrical current running through the experimental setup. Thus, clear behavioral evidence is necessary to understand whether glass eels use the geomagnetic field as a cue for orientation during their migration to freshwater.

We tested the innate orientation ability of European glass eels, newly arrived at the Norwegian coast, using a unique combination of laboratory and in situ observations. We conducted the tests using a drifting in situ chamber (DISC; Fig. 1) equipped with a circular arena in which glass eels were placed and their swimming and orientation were observed while the DISC drifted in situ in a fjord channel (Fig. 2). In addition, we submerged the arena in a circular tank in a magnetic laboratory on land, under manipulated simulated magnetic fields and with no other orientation cues (fig. S1). The data generated in these experiments were used to assess orientation of glass eels with respect to the magnetic field and the tidal cycle.

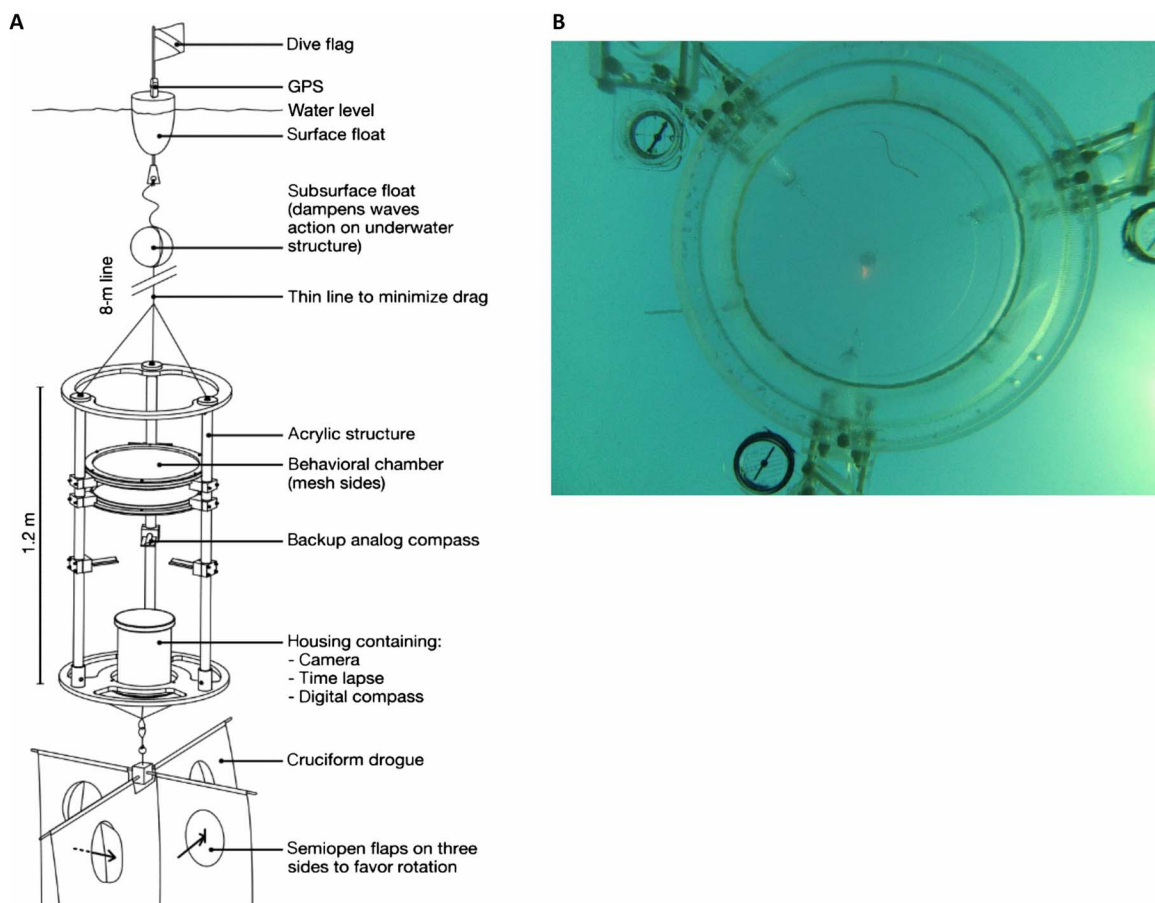


Fig. 1. Drifting in situ chamber. (A) The main underwater unit is composed of a chamber (of a size selected to accommodate the swimming abilities of the glass eels being tested), the imaging system, and a set of sensors. The DISC configuration for the glass eels was a 41-cm-diameter chamber placed 35 cm above the camera. General protocol: During deployment, the DISC was submerged alongside a small boat, and one animal was inserted through the top the chamber. The DISC was then slowly released at a selected depth and location for a duration of 20 min (5-min acclimation and 10-min observation). (B) Example of an image from the upward-looking camera showing the position of the glass eel inside the chamber, the three analog compasses, the water surface, and the downwelling sunlight as seen through Snell's window.

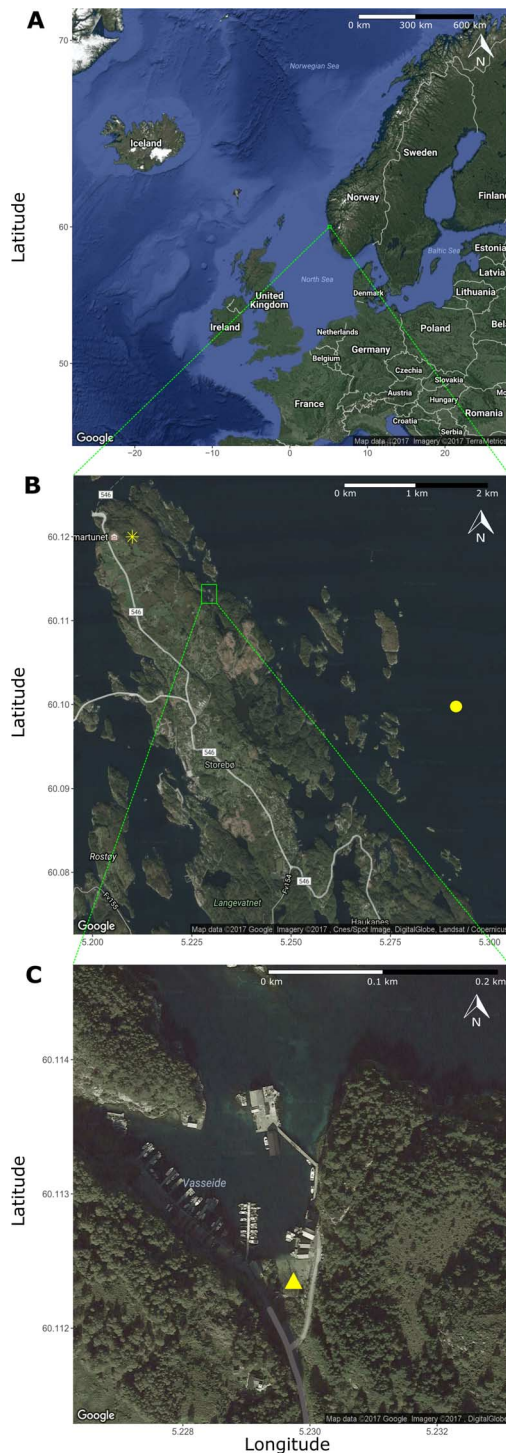


Fig. 2. Study location. (A) Northern Europe. (B) Austerøll location where experiments were conducted. The Austerøll archipelago is located between the North Sea (west) and the Bjørnafjorden fjord channel (east). The yellow circle (*) indicates the site of the in situ experiments, and the yellow asterisk (*) represents the location of the magnetic laboratory facility. (C) Zoomed satellite image of the stream estuary. The yellow triangle (▲) indicates the location of the stream estuary where *A. anguilla* glass eels were collected. The brown zone between the triangle and the water is a rocky gravel intertidal area. The map was created using RStudio version 0.98.1103 (package ggmap, 2009–2014, RStudio Inc.) (www.rstudio.com). Source of the images: Google Maps.

RESULTS

The orientation behavior of glass eels was observed, one eel at a time; most exhibited a preferred compass direction. Furthermore, glass eels oriented with the magnetic field and changed their preferred direction with respect to the tidal phase (Fig. 3).

We tested each eel twice, equally distributing the number of tests between ebb and flood tides, over a period of 7 days (see tables S1 and S2). Thus, we tested each eel once during one tidal phase in situ and once during one tidal phase in the magnetic laboratory. The swimming speed of the glass eels did not change between the tidal phases or between in situ and laboratory testing (fig. S2).

In situ

For the in situ experiments, we deployed the DISC in the sea, where it was allowed to drift with the current. We tested 54 glass eels, placing each glass eel in the DISC's circular transparent arena and recording their orientation behavior with a video camera. Through video-tracking analysis of the images, we computed the mean compass orientation of each glass eel (see Materials and Methods for more details). We found that during the tests, glass eels tended to explore the environment, moving continuously around the edges of the arena. This behavior created noise in the accuracy of the directionality, resulting in some low Rayleigh's r values from the analysis of the orientation at the individual level (see tables S3 and S4). However, the distribution of the positions of the eels indicated that each animal displayed a specific section of the chamber (Rayleigh's $P < 0.05$); the mean position was interpreted as a preferred bearing. At the individual level, 98% oriented in a preferred compass direction (Rayleigh test, $P < 0.05$; Fig. 3, A and B, and table S3). The eels tested during ebb tide showed a common orientation to the south ($n = 27$; Rayleigh's $P = 0.02$, $r = 0.38$; Fig. 3B), whereas the ones that were tested during flood tide did not exhibit a common orientation ($n = 26$; Rayleigh's $P = 0.43$, $r = 0.18$; Fig. 3A).

Magnetic laboratory

In the laboratory, 49 of the same glass eels that were tested in situ were observed in the DISC, which was submerged in a black tank inside a magnetic coil system (see the Supplementary Materials). The magnetic coil system made it possible to test each eel with a different configuration of the simulated magnetic field: The magnetic north in the laboratory was reoriented toward one of the four cardinal points of Earth's magnetic field in each test (fig. S3). The orientations of the glass eels were significant at the individual level (Fig. 3, C and D), with 35 of the 49 eels displaying orientation (71%; Rayleigh test, $P < 0.05$; table S4).

During ebb tide, the eels tested in the laboratory showed the same common orientation as observed during the in situ experiments, orienting to the south ($n = 15$; Rayleigh's $P = 0.04$, $r = 0.46$; Fig. 3D). However, in addition, they also oriented significantly during flood tide, but toward the opposite direction, to the north ($n = 20$; Rayleigh's $P = 0.02$, $r = 0.43$; Fig. 3C).

DISCUSSION

The objectives of the experiments were to observe how glass eels orient in their environment and to test whether they can use the magnetic field as an orientation cue. To address these questions, we tested the orientation abilities of glass eels in a transparent circular arena, which was allowed to drift in a fjord channel. The same

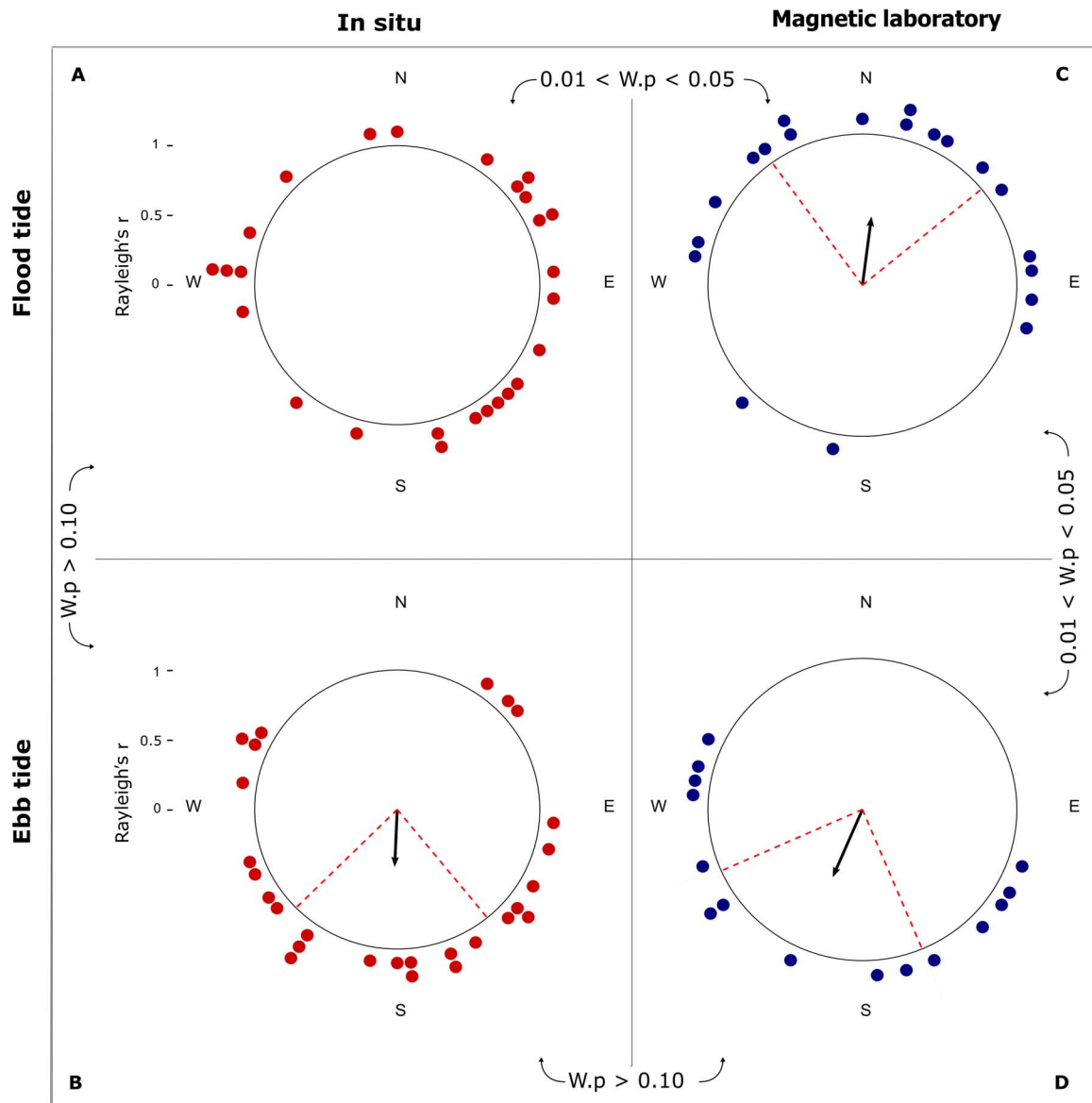


Fig. 3. Orientation of *A. anguilla* glass eels in situ and in the magnetic laboratory. The mean values of the individual bearing angles are presented as red dots for the eels tested in situ and blue dots for the eels tested in the magnetic laboratory. N, E, S, and W represent the four main magnetic cardinal points. The length of the black arrows corresponds to the Rayleigh r value in each graph and their orientation to the mean group direction. Red dashed lines indicate 95% confidence intervals. When the arrow and dashed lines are present, there is a significant directionality in orientation at the population level, according to the Rayleigh test of uniformity (5%). W.p are P values of the Watson's two-sample test of homogeneity. (A) Orientation of glass eels observed in situ during the flood tide ($n = 26$; Rayleigh's $P = 0.43$, $r = 0.18$). (B) Orientation of glass eels observed in situ during ebb tide ($n = 27$; Rayleigh's $P = 0.02$, $r = 0.38$). (C) Orientation of glass eels observed in the magnetic laboratory during flood tide ($n = 20$; Rayleigh's $P = 0.02$, $r = 0.43$). (D) Orientation of glass eels observed in the magnetic laboratory during ebb tide ($n = 15$; Rayleigh's $P = 0.04$, $r = 0.46$). The orientation behavior in (C) and (D) was displayed by the glass eels tested under rotated magnetic fields under laboratory conditions.

eels were then tested in the same arena under manipulated magnetic fields in the laboratory. To investigate the possible role of the tidal phase in the orienting behavior of glass eels, we conducted the tests during ebb and flood tides.

Glass eels exhibited a common orientation to the magnetic field whether they were in the sea or in the laboratory. Glass eels did not display any common orientation in situ during flood tide, but they oriented toward the south during ebb tide. In the laboratory, glass eels only had the magnetic field as an orientation cue, and they showed the same southward orientation during ebb tide. During flood tide, glass

eels oriented toward the north. From these results, we conclude that glass eels can perceive the magnetic field and that they use it as a magnetic compass to orient their movements. In the laboratory, they displayed a tidally dependent orientation, and their directionality during ebb tide was consistent with that observed in situ during the same tidal phase, despite the fact that they could not sense the changes in the tide. This implies that their compass orientation is associated with an endogenous rhythm linked to the ambient tidal cycle.

In the laboratory, we manipulated the magnetic field rotating the magnetic vector on the horizontal plane, resulting in different directions

of the magnetic north with respect to Earth's magnetic north. Under all configurations of the field, glass eels oriented using the rotated magnetic field as a frame of reference. This allowed us to control for any nonmagnetic bias (visual or olfactory), leaving only the magnetic field as an orientation cue.

Eels are widely distributed from continental Northern Norway to Northern Africa and far into the Mediterranean. At some point during their drift, glass eels must shift to a so-called "y axis orientation": The fish orient at right angles to the shoreline, which is designated as the x axis (40). In the sea, where there are no visual cues, this type of orientation is only possible with the use of a reference system such as the sun or the magnetic field. Because glass eels are active at night (41, 42), using the latter has obvious advantages. As glass eels get closer to the shore, olfactory cues from freshwater plumes and inland water odors would also guide them (43, 44).

Here, all the individuals were collected as they were entering a small stream (Fig. 2, A and B). The south-north directionality that they exhibited during the experiments might be consistent with the hydrodynamic conditions at the site where the eels were collected, because the estuary of the stream is oriented toward the north. Although we cannot make definitive conclusions about the significance of their preferred orientation based on the present experiments, indirect evidence for this common orientation exists from Pacific sockeye salmon (*O. nerka*), whose migratory route toward the continent can be predicted using the drift of the geomagnetic field (45). Other fish species can detect the magnetic field and use it as a directional cue during migration. For example, adult yellowfin tuna (*Thunnus albacares*) can distinguish between geomagnetically relevant magnetic fields (46), and juvenile sockeye salmon (*O. nerka*) imprint the intensity of the magnetic field characterizing the area where they first encounter seawater (45). As adults, salmon use this magnetic information during the long-distance phase of their migration to find their natal rivers (29, 45).

Glass eel orientation behavior was related to tidal phase. Like many other catadromous fishes, eels use selective tidal stream transport (STST) during the first phase of their upstream migration (18, 47–49). Glass eels rise in the water column during flood tide and drift passively toward the shore but swim at the sea bottom during ebb tide to migrate inshore and to avoid being carried back out to the open ocean (50–54). This behavior reduces the energetic cost of horizontal movement in coastal and estuarine areas (55). Our in situ results are consistent with this scenario. Glass eels did not show any common orientation during flood tide. During this tidal phase, they would take advantage of the local current and drift toward the shore, and therefore would not need to orient. During ebb tide, on the other hand, they oriented in a specific direction, and this is consistent with the counter-current behavior they would adopt to reach the shore or to avoid being pushed back out to the sea.

Glass eel orientation was consistently related to tidal phase in the laboratory, in the absence of any environmental cues. Orientation and swimming behavior linked to endogenous rhythms have been reported in various taxa. The vertical migration of the pelagic larvae of the estuarine crab, *Rhithropanopeus harrisi*, is modulated by the lunar phase; the crabs rise during flood tide and descend during ebb tide when tested under laboratory conditions (56). Further examples come from the intertidal crustacean *Eurydice pulchra*, which exhibits swimming patterns regulated by an independent circatidal pacemaker (57). Furthermore, circalunar endogenous rhythms can influence or entrain the magnetic orientation of animals. The turning

pattern of the flatworm *Dugesia dorotocephala* is related to the lunar phase and is affected by manipulation of the surrounding magnetic field (58). This relationship between magnetic orientation and lunar phase has also been observed in marine animals. For example, when placed in a Y-maze, the opisthobranch *Tritonia diomedea* makes choices that are related to the geomagnetic field and are linked to the lunar phase (59). The tidally dependent orientation of glass eels observed in situ persisted under laboratory conditions, even in the absence of cues such as odor, salinity, or tidal ellipse and turbulence, suggesting that the mechanism underlying the observed tidally dependent orientation is likely an internal rhythm. Glass eels observed in artificial flumes displayed rhythmic swimming, the periodicity of which was synchronized to the tidal phase (51). Moreover, glass eels of *A. rostrata* collected in tidal areas and tested in the laboratory showed a circatidal periodicity of 12.5 hours in their swimming behavior (60). These findings support the hypothesis that the tidal orientation of glass eels depends on internal stimuli rather than environmental cues. During flood tide, eels were significantly oriented only in the laboratory. In the sea, eels could have integrated magnetic cues with additional information, such as celestial and chemical cues. Conversely, when tested in the magnetic laboratory, eels displayed an orienting response based only on the magnetic compass system (that is, no other cues were available), and therefore, they might have used a different strategy to find freshwater outlets. Glass eels rely on salinity gradients as they arrive near fresh water (61, 62), and reversing directions with the current could allow them to cover a larger perimeter in search of chemical cues.

The tidal phase-linked magnetic orientation of glass eels that we observed is consistent with the well-documented behavior of glass eels in terms of how they use STST or a tidal-related signal (for example, odor and salinity gradient) to migrate toward freshwater habitats. Therefore, management measures, such as stocking of glass eels in European regions where eels are most depleted, should consider the ability of the eels to orient magnetically with respect to their environment. This could improve the chances that the eels will correctly integrate spatial cues that may be useful later in their life cycle. If eels are able to record magnetic features during their shoreward migration as glass eels, they could potentially use this information for orientation later in life, for example, on their migration back to the spawning areas.

CONCLUSION

Glass eels have a magnetic compass, and their orientation abilities appear to be linked to the tidal phase. This is preliminary evidence that magnetic compass-guided movement behavior could be tuned by an endogenous rhythm in the early life stages of a fish. This compass-guided movement, regulated by an endogenous rhythm, may be present in many migratory species.

MATERIALS AND METHODS

In situ experiments

In situ observations were conducted in a fjord channel situated between the island of Huftarøy (Norway) and the mainland. The 54 glass eels that were used in the deployments were collected just before they migrated up a small freshwater stream situated at 60.1122°N and 5.2298°E (Fig. 2). The collection site was an intertidal area with a rocky gravel bottom at the outflow. Eels were hiding under small

rocks and were collected with small hand nets. The glass eels' behavior was observed in situ using the DISC (Fig. 1) (63, 64). This drifting system is equipped with a semiopen circular chamber, transparent to both small-scale turbulence and light. Glass eels in the DISC were filmed in their natural environment while monitoring external environmental cues. The device is equipped with a GoPro camera, a HOBO light and temperature sensor, a Global Positioning System (GPS) device, three analog compasses, and a custom Arduino digital compass. The Orientation with No Frame of Reference (OWNFOR) (63) approach was applied to characterize the orientation of the glass eels in the apparatus while it was drifting.

We conducted 15-min orientation tests on the glass eels, considering the first 5 min as an acclimation period. Tests were performed over a period of 7 days, and distributed equally between ebb and flood tides (see tables S1 and S2). Tidal data were obtained from the tidal station BERGEN (ID 58; 60.3980°N, 5.3205°E; country, Norway; coastline, 040; station, 221). During each test, one individual was deployed in the DISC, and its movement was recorded by a GoPro camera, capturing video at 1 frame/s. The pictures were georeferenced with respect to the geomagnetic cardinal points, against the reference of the digital compass and the GPS device. The DISC was deployed in the fjord of Langenuen (northeast of Austevoll; ~60.09°N, ~5.28°E; salt water), where it drifted with the current at an average speed of 0.09 m s⁻¹ at a depth of 3 m in water that was 100 to 200 m deep, 800 to 1000 m distant from the coast, at a water temperature of 6° to 7°C. The DISC was allowed to rotate, and the position of the eels was monitored with the compasses. The video was processed by the DISCR (drifting in situ chamber user software in R) tracking procedure (see the Supplementary Materials), using R and a graphical user interface provided by ImageJ software (65, 66). We collected positional data and bearings (in units of magnetic degrees) of individual glass eels with respect to the center of the chamber at a rate of 1 frame/s.

Data analysis consisted of two steps. First, the mean orientation of each individual was computed from the bearings collected by the video-tracking analysis. The ability of each individual to keep a specific bearing in the DISC was considered to be evidence of directionality. We assessed the significance of the directionality using the Rayleigh test of uniformity ($P < 0.05$) and the level of convergence of the bearings toward one direction by the Rayleigh test r value (from 0 to 1) (65, 66). Second, we assessed the significance of the directionality at the group level (that is, the overall directionality of all the individuals tested) to evaluate the common orientation of the glass eels. To accomplish this step of the analysis, we applied the Rayleigh test of uniformity to the values of all the mean individual bearings.

Experiments under simulated and manipulated magnetic fields

To further assess whether the orientation of glass eels was related to the geomagnetic field, we conducted experiments at the Institute of Marine Research's magnetic research facility (60.1175°N, 5.2118°E; Hufthamar, Austevoll, Norway). We used 49 of the same eels that were tested in situ.

The magnetic laboratory is designed to study the magnetic orientation of aquatic animals. It is equipped with a triaxial electric coil system (see fig. S1A), with a design described by Merritt *et al.* (67), connected to a power supply (maximum, 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. S1A) filled with seawater, which is

pumped from the sea 300 m away. The building (see fig. S1B) 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). The experiments in the laboratory followed the same protocol as those in situ. The same DISC was submerged in the circular dark tank (see fig. S1C), and each eel was recorded for 15 min, with the first 5 min considered as an acclimation period. The laboratory is equipped with two nested electric coil systems. 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 μ 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 μ T and 73°, with a deviation of <1°). Tests were carried out under four simulated magnetic field conditions where magnetic north was reoriented to the geographical east, south, west, and north (see fig. S3). Each glass eel experienced only one of the four magnetic conditions. Using this approach, we eliminated any nonmagnetic cue that could have influenced the orientation response of the animals. The number of tests conducted was equally distributed between ebb and flood tides that occurred in the ocean during the trials (although eels could not detect the currents in the magnetic laboratory).

Statistical analysis

The significance of the directionality at both the individual level (first order) and population level (second order) was assessed using the Rayleigh test of uniformity. We used Watson's two-sample test for homogeneity for circular data for the comparison between the global orientations (Fig. 3). Tests were performed using R, packages "discr" and "circular." In all tests, a P value of <0.05 was considered significant.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/6/e1602007/DC1>

The magnetic laboratory

Analysis and data collection in R

Activity level of the animals

Protocol of the tests with the DISC in situ in the fjord

Collection and maintenance of the glass eels

Statistics

Details of the tests

Analysis of the orientation at the individual level

Magnetic laboratory protocol details

fig. S1. Magnetic laboratory facility and the DISC inside the experimental tank.

fig. S2. Swimming speed of glass eels tested.

fig. S3. Schematic diagrams of the magnetic protocol.

table S1. Day, hour, and tidal phase of the tests conducted in situ.

table S2. Day, hour, and tidal phase of the tests conducted in the magnetic laboratory.

table S3. Mean orientation of the glass eels tested in situ.

table S4. Mean orientation of the glass eels tested in the magnetic laboratory.

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