

# A Magnetic Map Leads Juvenile European Eels to the Gulf Stream

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## SUMMARY

Migration allows animals to track the environmental conditions that maximize growth, survival, and reproduction [1–3]. Improved understanding of the mechanisms underlying migrations allows for improved management of species and ecosystems [1–4]. For centuries, the catadromous European eel (*Anguilla anguilla*) has provided one of Europe's most important fisheries and has sparked considerable scientific inquiry, most recently owing to the dramatic collapse of juvenile recruitment [5]. Larval eels are transported by ocean currents associated with the Gulf Stream System from Sargasso Sea breeding grounds to coastal and freshwater habitats from North Africa to Scandinavia [6, 7]. After a decade or more, maturing adults migrate back to the Sargasso Sea, spawn, and die [8]. However, the migratory mechanisms that bring juvenile eels to Europe and return adults to the Sargasso Sea remain equivocal [9, 10]. Here, we used a “magnetic displacement” experiment [11, 12] to show that the orientation of juvenile eels varies in response to subtle differences in magnetic field intensity and inclination angle along their marine migration route. Simulations using an ocean circulation model revealed that even weakly swimming in the experimentally observed directions at the locations corresponding to the magnetic displacements would increase entrainment of juvenile eels into the Gulf Stream System. These findings provide new insight into the migration ecology and recruitment dynamics of eels and suggest that an adaptive magnetic map, tuned to large-scale features of ocean circulation, facilitates the vast oceanic migrations of the *Anguilla* genus [7, 13, 14].

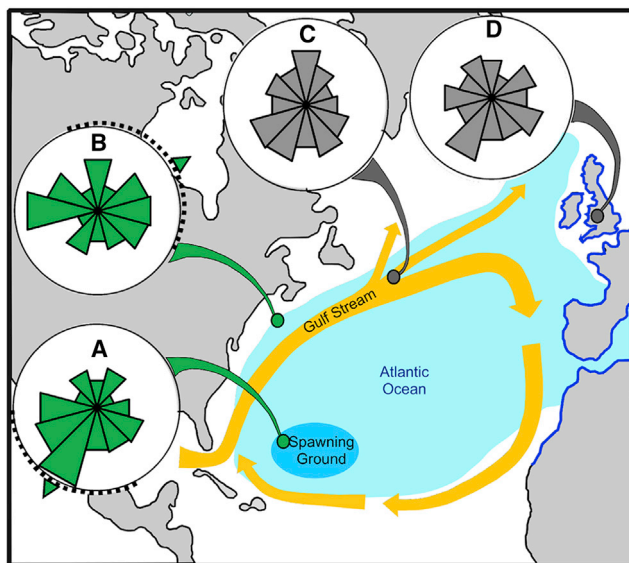
## RESULTS

### The Eel Magnetic Map

We performed a “magnetic displacement” experiment near Brecon, Wales (United Kingdom) using glass eels (*Anguilla anguilla*) captured in the Severn Estuary after completing their marine migration [6]. We exposed juvenile eels to four magnetic fields marking regions where oriented swimming might influence transport along the Gulf Stream System, their oceanic migratory pathway (Figure 1). We observed a significant difference in the orientation of eels in the four magnetic fields (chi-square test:  $\chi^2 = 50.9$ ,  $df = 33$ ,  $p = 0.039$ ), providing the first demonstration that eels use geomagnetic map information to orient. A field corresponding to the Sargasso Sea breeding grounds elicited southwestward orientation (median heading =  $210^\circ$ ;  $\chi^2 = 32.2$ ,  $df = 11$ ,  $p < 0.001$ ,  $n = 205$ ), while a field from the northwest Atlantic elicited northeastward orientation (median heading =  $60^\circ$ ;  $\chi^2 = 24.1$ ,  $df = 11$ ,  $p = 0.012$ ,  $n = 200$ ). A magnetic field from the northern mid-Atlantic and the ambient field at the test site elicited orientation indistinguishable from random ( $\chi^2 < 11.5$ ,  $df = 11$ ,  $p < 0.405$  for both,  $n = 223$  and  $212$ , respectively).

### The Magnetic Map Aids Migration

To place observed orientation responses into an environmental context, we performed numerical simulations using an ocean circulation model [15]. Virtual juvenile eels were released as particles in the Sargasso Sea, northwest Atlantic, and northern mid-Atlantic at three depths (30, 150, and 300 m) during three years (2000, 2005, and 2010). For the two regions for which significantly non-random orientation was observed during the magnetic displacement experiment, simulations of passive drift were compared to simulations of weak swimming (2.5 cm/s [16]) in the directions taken by eels in the corresponding magnetic fields. Across 18 pairwise comparisons, oriented swimming increased the number of virtual eels entering the Gulf Stream System by an average of 48% (range: 3%–122%) compared to passively drifting virtual eels (Wilcoxon signed-rank test:  $p < 0.01$ ,  $n = 9$ , for the Sargasso Sea and northwest



**Figure 1. Oriented Movement of Juvenile Eels Exposed to Magnetic Fields from Four Locations along Their Marine Migration Route**

(A) is the Sargasso Sea, (B) the northwest Atlantic, (C) the northern mid-Atlantic, and (D) the ambient field in Wales, United Kingdom. The radial histograms scale to the proportion of eels moving into each 30° escape section (see also Figure S1); the outer circle equals 16% of the total number of eels tested in each field. The green radial histograms indicate eel orientation that was significantly non-random. For non-random orientations, outer triangles are the median heading and dotted lines the 25% quartiles (A and B; Table S1). The blue oval represents the approximate location of the spawning ground where the smallest larvae were found (<10 mm), and the large light-blue shaded area represents the range of eel larvae reported by Schmidt [7]. Areas of coastline outlined in blue indicate the distribution of the coastal and freshwater life stages. Significant pairwise differences among treatments were observed between the northwest Atlantic field (B) and the Sargasso Sea (A) and northern mid-Atlantic fields (C) (chi-square test:  $\chi^2 > 22.74$ ,  $p < 0.019$ ,  $df = 11$ ; for the two pairwise comparisons B-A and B-C).

Atlantic; Figure 2; Table S2). From the Sargasso Sea, 9.77% (range: 1.39%–16.97% depending on year and depth) of passive particles entrained in the Gulf Stream System, compared to 14.42% (range: 3.09%–24.24%) of those programmed to swim. Similarly, passive drift resulted in 10.42% (range: 5.37%–19.13%) of particles entraining into the Gulf Stream from the northwest Atlantic, whereas simulating swimming increased this to 14.08% (range: 8.13%–24.35%). In the northern mid-Atlantic, 70.10% of passive particles (range: 57.11%–75.65%) moved eastward with the Gulf Stream System. Oriented swimming was not simulated in this region, as eel orientation in the corresponding field was random.

## DISCUSSION

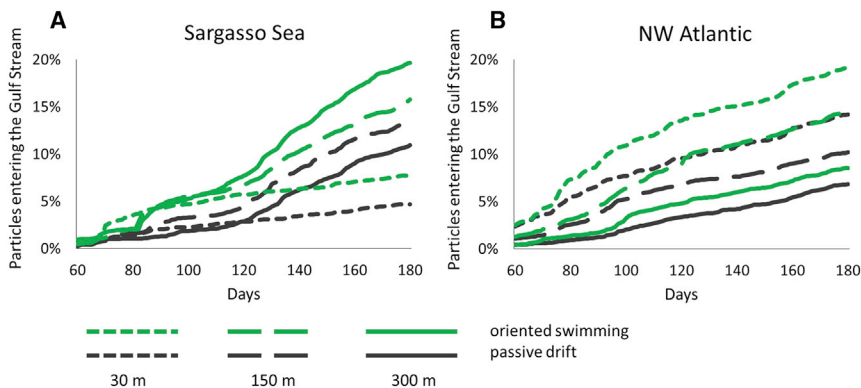
While eels are known to be sensitive to electromagnetic fields [17–19], our results provide the first evidence that they derive positional information from the Earth’s magnetic field. We show that juvenile European eels possess a magnetic map that allows them to modify their orientation to take advantage of consistent ocean circulation features along their marine migration route. Specifically, southwestward swimming from the Sargasso Sea

breeding location would result in eels moving into the Antilles Current and northwest into the Gulf Stream System [20]. In the northwest Atlantic, swimming northeastward would decrease the chances of eels entering or remaining near North America and would facilitate movement eastward with the northern limb of the Gulf Stream. Thus, the magnetic map in juvenile eels appears tuned to promote transport out of the western Atlantic via the Gulf Stream System, which provides an energetically efficient route toward Europe. Our findings further suggest that as eels reach the eastern Atlantic, arrival to European rearing habitats becomes increasingly certain and natural selection for oriented swimming is relaxed [21]: orientation was random in the field marking the northern mid-Atlantic, and our simulations showed a high probability (~70%) of eastward transport of passively drifting particles in this region.

Our experiments indicate that eels use both intensity and inclination of the magnetic field, perhaps as a bicoordinate map [11, 22–25], to resolve their position at relatively fine spatial scales (Figure 3). Eels experiencing only a change in total field intensity (relative to ambient, intensity increased by 4.9%) orient differently than eels experiencing only a change in inclination (inclination decreased 3.0%) (Figure 1; Table S1). Given such sensitivity to magnetic map information, our results offer a plausible explanation for the complex migration ecology of North Atlantic *Anguilla* species, whereby juvenile European and American (*A. rostrata*) eels arrive at rearing habitats on opposite sides of the Atlantic despite adults spawning in partial sympatry in the Sargasso Sea [2, 3, 26, 27]. Larvae of the two species could use magnetic maps to differentially orient swimming in the western Atlantic to position themselves in currents that favor transport toward either Europe or North America. Likewise, our findings provide a compelling possibility for how adult anguillid eels return to oceanic spawning grounds from distant coastlines [13, 14, 28].

Though our results present clear evidence for a magnetic map in juvenile eels, we observed substantial variation in orientation among individuals. Though such variation is common in magnetic displacement experiments [11, 12], motivation to orient in response to changes in the magnetic field may have been reduced in glass eels that had already completed their marine migration as compared to younger eels. However, variation in orientation may also reflect an adaptive response to natural selection [29]. As revealed by our simulations, the advantage of oriented swimming differs between years, depths, and regions (Figure S2), a variable selective regime that should favor “generalist” rather than “specialist” navigational strategies [30]. Similarly, variation in the orientation response of juvenile eels is consistent with a bet-hedging strategy: adult eels may produce offspring with a variety of orientation responses to mitigate environmental stochasticity, such as shifts in climate and geographic drift of the Earth’s magnetic field [31].

The growing list of long-distance marine migrants that extract positional information from the magnetic field [11, 25, 32, 33] implicates the magnetic map as a key mechanism by which organisms orient swimming at ocean-basin scales. The phylogenetic diversity of animals that derive positional information from the geomagnetic field, including those undertaking shorter migrations [12, 24, 34, 35], suggests that the ability to use a magnetic map is either deeply conserved or has evolved multiple times. Identifying the genetic basis of the magnetic map, quantifying



of 30, 150, and 300 m, respectively, within the Global Hybrid Coordinate Ocean Model. For clarity, each line corresponds to the three-year average for simulations performed using ocean currents observed in 2000, 2005, and 2010 (full results shown in Figure S2 and Table S2). Pairwise comparisons by year and depth at 180 days indicate that simulating observed swimming orientations significantly increased entrainment of virtual eel larvae into the Gulf Stream (Wilcoxon signed-rank test:  $p < 0.01$ ,  $n = 9$ ; for each region).

heritable variation in orientation, and determining how its expression varies through ontogeny are outstanding research challenges [29] that will provide a richer evolutionary context for understanding the ecology of marine migrants and improve management of the fisheries they support [2, 36, 37].

## EXPERIMENTAL PROCEDURES

### Permission and Animal Welfare

Eel husbandry was approved by Natural Resource Wales and followed the guidelines of the Association for the Study of Animal Behaviour and the Animal Behavior Society. The procedures used in the magnetic displacement experiment were not subject to regulation under UK Home Office guidelines.

### Magnetic Displacement Experiment

Juvenile glass eels collected from the Severn Estuary (N 51° 50' 41.46", W 2° 15' 53.98") were transported to the Natural Resources Wales Fish Culture Unit near Brecon, Wales (N 51°, W 3°) on April 28, 2015. Eels were housed in well water in a 3,000 L tank (height 100 cm, diameter 200 cm) at 26°C to encourage feeding and growth during the transition to captive rearing. The dissolved oxygen level in the rearing tank was maintained above 70% saturation using an aeration system. Ammonia, nitrite, and nitrate levels remained below 0.1 ppm. Eels were fed a mixed diet of cod roe and fish pellets twice daily. At testing, eels ranged 6.9 to 7.4 cm in length.

In the rearing tank, the total field intensity along magnetic north ranged from 36.2  $\mu\text{T}$  to 49.7  $\mu\text{T}$ . Owing to potential disorientation due to spatial heterogeneity in the magnetic field [33], eels were housed away from magnetic anomalies 2 days prior to testing (total field intensity 49.1  $\mu\text{T}$ , inclination 66°). Magnetic field measurements were taken with a single-axis fluxgate magnetometer (resolution:  $\pm 5$  nT) following nullification within a zero Gauss chamber. Temperature and dissolved oxygen in the pre-testing tanks (150  $\times$  50 cm) were kept the same as in the rearing tanks. Eels were not fed during the pre-testing period.

The experiment was conducted from June 3 to July 4, 2015, between 0800 and 1700 hr. Magnetic fields were created using two four-coil systems arranged orthogonally, one along the north-south axis and the other in the vertical plane [11]. Each coil system was controlled by an independent DC power supply using constant current. Orientation arenas (Figure S1) were placed on a platform at the center of the magnetic coil system (ambient field: total field intensity 49.1  $\mu\text{T}$ , inclination angle 66°) and filled with 15 cm of water (26°C) from the same source as the rearing and pre-trial tanks. Each of the 16 arenas (25 cm diameter) comprised a central holding cylinder filled with water (12 cm diameter), a removable plastic settling cylinder (5 cm diameter), and 12 equal-area outer sections corresponding to 30° on a compass. One of four test fields was randomly selected: (1) the ambient field of the test site,

### Figure 2. Ocean Circulation Model Simulation Results for the Percentage of Virtual Eels Entering the Gulf Stream during Passive Drift and Oriented Swimming

(A) is for particles released at the location of the Sargasso Sea experimental field, and (B) is for particles released at the location of the northwest Atlantic experimental field (Figure 1). The black lines show entrainment probability for passively drifting particles. The green lines show entrainment probability for particles programmed to swim southwestward (A) and northeastward (B) in the direction observed in the magnetic displacement experiment (Figure 1) at a conservative [16] swimming speed of 2.5 cm/s. Dotted, dashed, and solid lines represent results from simulations at depths

(2) a field characteristic of the western Sargasso Sea (N 28°, W 78°; total field intensity 43.9  $\mu\text{T}$ , inclination angle 55°), (3) a field characteristic of the northwest Atlantic (N 40°, W 73°; total field intensity 51.5  $\mu\text{T}$ , inclination angle 66°), and (4) a field characteristic of the northern mid-Atlantic (N 46°, W 45°; total field intensity 49.1  $\mu\text{T}$ , inclination angle 66°) (Table S1). Field values were determined using the International Geomagnetic Reference Field (IGRF-12) [38]. Field uniformity of the induced magnetic fields was better than  $\pm 0.5\%$  across the 16 locations on the testing platform. Eels from the pre-test tanks were placed into the center of the orientation arenas (one eel per arena) inside the plastic settling cylinder. The settling cylinder prevented movement of the eel into the outer sections during the 10 min acclimatization period under ambient magnetic field conditions [11, 21]. The selected test field was activated and eels were given another 10 min to acclimatize to the new field before the settling cylinder was removed. Eels were then given 10 min to leave the central holding section and enter one of the 12 outer sections, at which point their orientation choice was recorded. Each eel was used once. All arenas were sprayed with 70% ethanol and rinsed with well water between trials in order to remove olfactory cues that might affect subsequent trials. Arenas were placed in the same position and orientation between trials. The magnetic coil was covered with black shade cloth to minimize stress to the eels and maintain water temperatures.

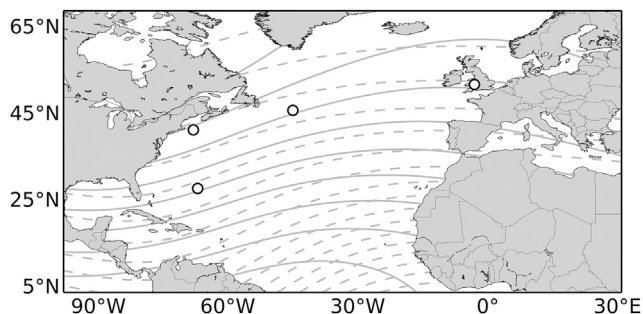
Eels that remained in the central holding section were excluded from analyses. Thus, sample sizes were 212 eels for the ambient field, 205 for the Sargasso Sea field, 200 for the northwest Atlantic field, and 223 for the northern mid-Atlantic field. This resulted in slightly uneven numbers of eels tested at particular times of day and on particular dates for the four treatments. However, neither time of day nor date was related to eel orientation (circular correlation:  $r < 0.058$ ,  $p > 0.093$ ,  $n = 840$ ; for both time of day and date). Thus, differences observed among treatments are unlikely to result from temporal variation in non-magnetic conditions.

Orientation data were analyzed using non-parametric statistics in Oriana v.2. A multi-sample chi-square test was performed to determine whether eel orientation differed among the four test fields. Pairwise chi-square tests were performed to assess the sensitivity by which eels could discriminate magnetic fields (i.e., a significant difference in orientation between two test fields implies that the resolution of the magnetic map of eels is at least as fine as the difference between those fields). A chi-square test was performed on each treatment to assess whether orientation could be distinguished from random. For non-random distributions ( $p < 0.05$ ), the median heading and 25% quartiles were computed for input into the ocean circulation model simulations.

### Ocean Circulation Model Simulations

Virtual particles were tracked within the Global Hybrid Coordinate Ocean Model [15] (HYCOM) using ICHTHYOP (v.2) software [39]. Global HYCOM has output at 0000 hr GMT with a spatial resolution of 0.08° ( $\sim 7$  km at





**Figure 3. Map of Total Field Intensity and Inclination Angle Isolines across the North Atlantic**

The contours of intensity (solid, 3  $\mu$ T) and inclination angle (dashed, 6°) are based on the International Geomagnetic Reference Field (IGRF-12) for the year 2015. The white circles show geographic locations of the test fields used in the magnetic displacement experiment. The northwest Atlantic and the northern mid-Atlantic regions elicited significantly different orientation in eels but differ only slightly in field intensity (less than 5%) and inclination angle (less than 3%), suggesting that eels possess a magnetic map of relatively precise resolution.

mid-latitudes). The HYCOM reanalysis uses data assimilation to produce “hindcast” model output that reflects in situ and satellite measurements of oceanic features such as meandering currents, fronts, filaments, and eddies [15], which are important in realistically characterizing marine animal movements [21]. For advection of particles through HYCOM velocity fields, ICHTHYOP implemented a Runge-Kutta fourth-order time-stepping method whereby particle position was calculated every half hour [39].

Paired simulations were performed for the locations of the two magnetic displacement fields that elicited non-random orientation (i.e., the “Sargasso Sea” and “northwest Atlantic” fields only) [21, 31]. We compared the fate of particles that drifted passively or swam with the same orientation as was observed in the magnetic displacement experiment. To account for annual variability in ocean conditions and differences in ocean currents at the depths at which larval eels might migrate [5, 40], we performed nine simulations for each region covering three years (2000, 2005, and 2010) and three depth layers (30, 150, and 300 m). 15,000 virtual particles were released throughout the month of May for each of the 18 year-depth-behavior combinations and tracked for 180 days. In accordance with the quartiles around the median heading, particles programmed to swim in the Sargasso Sea region adopted headings between 150° and 270°, randomly changing within this range each time-step. In the northwest Atlantic region, particles adopted headings between 330° and 120°. Based on maps and growth curves presented in [7], larval eels are expected to average ~25 mm in body length in the western Atlantic during the late spring and early summer. Assuming a conservative swimming speed of ~1 body length per second, this corresponds to the 2.5 cm/s swimming speed chosen for our simulations (other models of larval eel swimming have assumed 0.5 to 4 body lengths per second [16]). For the Sargasso Sea simulations, particles were counted as entering the Gulf Stream if they crossed north of 25°N and west of 77°W. For the northwest Atlantic region, particles were counted as entering the Gulf Stream if they crossed north of 40°N and east of 53°W. Wilcoxon signed-rank tests were used to determine whether oriented swimming increased the probability of particles entering the Gulf Stream compared to simulations of passive drift after 180 days. To provide environmental context for the random orientation observed in the northern mid-Atlantic field, passive drift simulations were performed for this location.

#### ACCESSION NUMBERS

Information on the data underpinning the results presented here, including how to access them, can be found at Cardiff University data catalogue at <http://dx.doi.org/10.17035/d.2017.0033096803>.

#### SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and two tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.03.015>.

#### AUTHOR CONTRIBUTIONS

Conceptualization: S.L., N.F.P., J.F.S., and K.A.Y.; Methodology: L.C.N.-J., N.F.P., and K.A.Y.; Investigation: L.C.N.-J. (magnetic displacement experiment) and N.F.P. (migration simulations); Writing – Original Draft: L.C.N.-J. and N.F.P.; Writing – Review & Editing: all authors; Supervision: N.F.P. and K.A.Y.

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