

A unifying hypothesis for the spawning migrations of temperate anguillid eels

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Abstract

Anguillid eels grow in freshwater but spawn in the open ocean. The cues that guide eels over long distances to the spawning area are unknown. The Earth's magnetic field can provide directional and positional information and is likely used by catadromous eels during their spawning migration; as magnetosensitivity and compass orientation have been reported in eels. To test whether this is theoretically possible, we compared the migratory routes of five species of temperate eels that undertake long migrations with the geomagnetic field of their distribution/spawning areas. We found that, regardless of the species and although routes are different between life stages, larvae of those species always drift along paths of increasing magnetic inclination and intensity, while adults follow reverse gradients. This is consistent with an imprinting/retracing hypothesis. We propose a general navigation mechanism based on larvae imprinting on a target magnetic intensity (or inclination) at the hatching area and on the intensity (or inclination) gradient during larval drift. Years later, adults retrace the magnetic route by following the gradient of decreasing total intensity (or inclination) values that occurs towards lower latitudes. As they reach the target value, adults switch to compass orientation to stay on the target isoline and reach the spawning area. The proposed mechanism fits for all temperate eels examined. Knowledge about navigational strategies of eels is important to evaluate the effectiveness of management strategies that involve stocking of juveniles displaced from one area to another to rebuild local populations.

KEYWORDS

Anguilla sp., compass orientation, geomagnetic field, magnetic inclination, magnetic total intensity, secular variation

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1 | INTRODUCTION

Many fish undertake long distance migrations to feed and spawn. How these migratory species find their way to distant areas, across several thousand kilometres, is a mystery. Anguillid eels are characterized by long-distance migrations between growth habitats and spawning areas. All 19 species of anguillids (*Anguilla* sp., Anguillidae), also called freshwater eels, breed in open-ocean areas but spend their growth phase in coastal and freshwater habitats (Tesch, 2003). They are almost all panmictic (each species is structured as one population), having unique spawning areas that are located over deep water (Aoyama, 2009; Miller, 2009; Tesch, 2003; Tsukamoto et al., 2002). Anguillid eels also have in common that the exact time and location of their spawning site is either uncertain or unknown because spawning events have never been observed in the wild. For some species, approximate spawning locations have been identified by careful examination of the distributions of their leptocephalus larvae—or eggs in the case of the Japanese eel (*Anguilla japonica*)—collected during scientific surveys (e.g. Kuroki et al., 2020; Miller & Tsukamoto, 2017; Schmidt, 1922; Tsukamoto et al., 2011). In addition, sexually mature specimens of the *A. japonica* and the marbled eel (*A. marmorata*) have been collected, putatively on or near their spawning area (Chow et al., 2009; Kuroki et al., 2009; Miller & Tsukamoto, 2017; Tsukamoto, 2006; Tsukamoto et al., 2003, 2011; Yoshinaga et al., 2011).

Anguillid eels are, for the most part, widely distributed during their growth phase. For example, the European eel (*A. anguilla*) occurs in habitats between Norway and Morocco, but spawns in the Sargasso Sea (Als et al., 2011; Pujolar, 2013; Schmidt, 1922; Tesch, 2003). How eels find their way back to their unique spawning area is still a mystery. The orientation mechanisms needed for them to synchronize their migration so that they congregate at the same time and location, despite beginning their migration from such different starting points, have to be reliable and efficient over long distances and timeframes. Adult migrating eels swim in pelagic water at depths between 200 and 800 m (Aarestrup et al., 2009; Schabetsberger et al., 2016). At those depths in the open ocean there are few or no guideposts. Although oceanic/salinity fronts are present in the spawning areas of most Anguillid species (Aoyama et al., 2014; Kleckner & McCleave, 1988; Munk et al., 2010; Schabetsberger et al., 2016), these features are not precise or predictable enough to guide adult migrating eels to a common spawning area. Odours from hydrothermal activity have also been put forward as a possible cue (Chang et al., 2020). However, for the Atlantic eels, they do not align with the known distribution of leptocephalus larvae and cannot explain the full extent of the migration.

One possible cue that could guide the orientation of eels during their migration is the geomagnetic field. This environmental cue is omnipresent and is unaffected by time of day or oceanographic or weather conditions. It could guide eels as a “compass,” that is, a direction relative to magnetic North, but can also potentially provide positional information, that is, act as a kind of GPS (Lohmann

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et al., 2007). This “map” can be derived from components of the geomagnetic field, such as inclination (*I*), horizontal (*H*), vertical (*Z*) and total intensity (*F*), and/or declination, the values of which change gradually over the earth's surface. Many fishes can perceive magnetic field information (Cresci et al., 2019; Hellinger & Hoffmann, 2009; O'Connor & Muheim, 2017; Putman, Scanlan, et al., 2014; Quinn & Brannon, 1982; Shcherbakov et al., 2005; Walker, 1984; Willis et al., 2009). Compass orientation, manifested as changes in the swimming direction relative to the direction of magnetic north, has been demonstrated in the continental life-stages of *A. anguilla* (Cresci, 2020; Cresci et al., 2017; Durif et al., 2013). Whether eels use other components of the magnetic field, such as intensity and inclination (i.e. the magnetic map hypothesis), which could provide them with positional information during migration, remains unknown (Durif et al., 2017). Such a magnetic map has been demonstrated in many animals, including birds, butterflies, newts, spiny lobsters, salmon and sea turtles (Boles & Lohmann, 2003; Freake et al., 2006; Lohmann et al., 2007; Mouritsen, 2018; Munro et al., 1997; Phillips et al., 2002), but not as yet in eels.

True navigation requires that an organism forms a mental grid in relation to the target destination and adjusts its “compass” as it moves towards that destination (Phillips, 1996). The grid, or map, can be composed of two environmental gradients ideally aligned perpendicular to one another (Wallraff, 1990). These can be altitude, depth, temperature, for example, but can also be components of the geomagnetic field, such as inclination (I) and/or total intensity (F) (Gould, 1980). Both, F and I , decrease from the poles towards the equator in a North–South gradient. Thus, magnetic field isolines (representation on a map of the areas characterized by the same value of a magnetic field component) most often run parallel to each other along the East–West axis (Bostrom et al., 2012). This means that an animal can navigate along a North–South axis by using I or F . However, because there is no distinct gradient of either I or F over longitude, navigation based on this cue becomes more difficult when moving along the East–West axis. For example, it appears unlikely that *A. anguilla* could navigate back to its spawning area in the Sargasso Sea by following gradients of I or F .

Complicating the magnetic map hypothesis are the variations and drift in the Earth's magnetic field that occur over decades, so-called secular variation. Due to this, the geomagnetic characteristics of the geographical location of the target area (spawning area) will typically vary between generations of eels, or even during the life cycle of an individual eel. While imprinting this target location during the early-life stages (hatching and larval stage), versus inheriting it, could help solve this problem, it may not completely resolve it in the case of anguillid eels that have a long life cycle. For those eels, the initial magnetically imprinted location may correspond to a different geographical location when the eel undertakes its return migration up to 30 years later. Thus, while the geomagnetic field is often cited as the most probable environmental cue that could guide anguillid eels during their migrations, how eels could make use of it in practice has never been explained.

In this study, we investigated whether certain components of the geomagnetic field are available for eels to use as guidance cues in their migration between their growing and spawning areas and whether such patterns are consistent over the distribution area of different anguillid species. We present a comprehensive hypothesis on the orientation mechanisms of anguillid eels throughout their life cycle. Specifically, we propose that adult eels find their spawning areas by following the features of the magnetic field (both target values as well as magnetic field gradients) that they have imprinted during their migration towards the continental shelf as larvae and post-larvae. To test this hypothesis, we assessed (i) whether retracing the magnetic gradients along the migratory route of eel leptocephali is consistent with the migratory routes of adult eels on their way back to the spawning area; (ii) whether these gradients are consistent between different anguillid species present in both southern and northern hemispheres and (iii) how secular variation would affect the navigation accuracy of eels over the timeframe of their average longevity. To accomplish this, we used existing models to calculate the geomagnetic inclination and field intensity in four different oceans and examined the distributions of five temperate

species of eel, *A. anguilla*, *A. rostrata* (American eel), *A. japonica*, *A. australis* (short-finned eel), *A. dieffenbachii* (New Zealand longfin eel), to identify whether similar patterns of the geomagnetic field exist between their growing and spawning areas.

2 | METHODS

2.1 | Overview of the methods

To examine whether suitable magnetic gradients are present between the growth and the spawning area, we mapped the magnetic components (intensity F and inclination I) along with biological data (larval drift and known trajectories of returning adult eels) of five temperate eel species. Our conclusions are based on calculations of the ranges of values and the overlap between growth and spawning areas of different species as well as maps to assess consistency between species.

To evaluate the effect of secular variation on the potential displacement of eels we calculated the magnetic components at the spawning areas for different time intervals representing the lifecycle of an eel. We calculated the difference in total magnetic intensity and inclination between hatching and spawning ($\Delta F = F_{\text{hatch}} - F_{\text{spawn}}$; $\Delta I = I_{\text{hatch}} - I_{\text{spawn}}$) of a hypothetical eel born in 1900 and assumed several ages at maturation (or age at silvering). We did this for *A. anguilla*, *A. rostrata* and *A. japonica*, for which we have the most precise location of spawning areas. To determine relevant time intervals, we used information on age of eels at maturity (i.e. silvering). Silvering depends on growth and, therefore, on environmental conditions such as temperature. Eels in the southern part of the distribution mature at an earlier age than eels in the north (Daverat et al., 2012; Durif et al., 2009; Svedäng et al., 1996; Vøllestad, 1992). A rough average for silver *A. anguilla* females is 10 years in the south and 20 years in the north (Durif et al., 2009, 2020; Poole & Reynolds, 1996). Silver males are much smaller and younger and migrate at approximately 5 years of age in the south and 10 years in the north (Durif et al., 2009). Actual ranges are 3 and 57 years for females and between 2 and 33 years for males (Durif et al., 2009; Poole & Reynolds, 1996). Therefore, we calculated ΔF and ΔI between 5 and 50 years, at intervals of 5 years. We used the same range/intervals for the *A. japonica* silver eels, although they are much younger (approximately 9–10 years; Yokouchi et al., 2012).

2.2 | Study species and their spawning areas

All anguillid eels are characterized by five life stages whose durations vary according to the species: (a) the larval phase or leptocephalus which is fully oceanic; (b) the glass eel stage which begins when eels approach the continent and during which they actively orient towards the coastline and freshwater habitats; (c) the yellow eel stage which is the continental phase during which eels grow and accumulate fat; (d) the silver eel stage during which eels migrate towards the

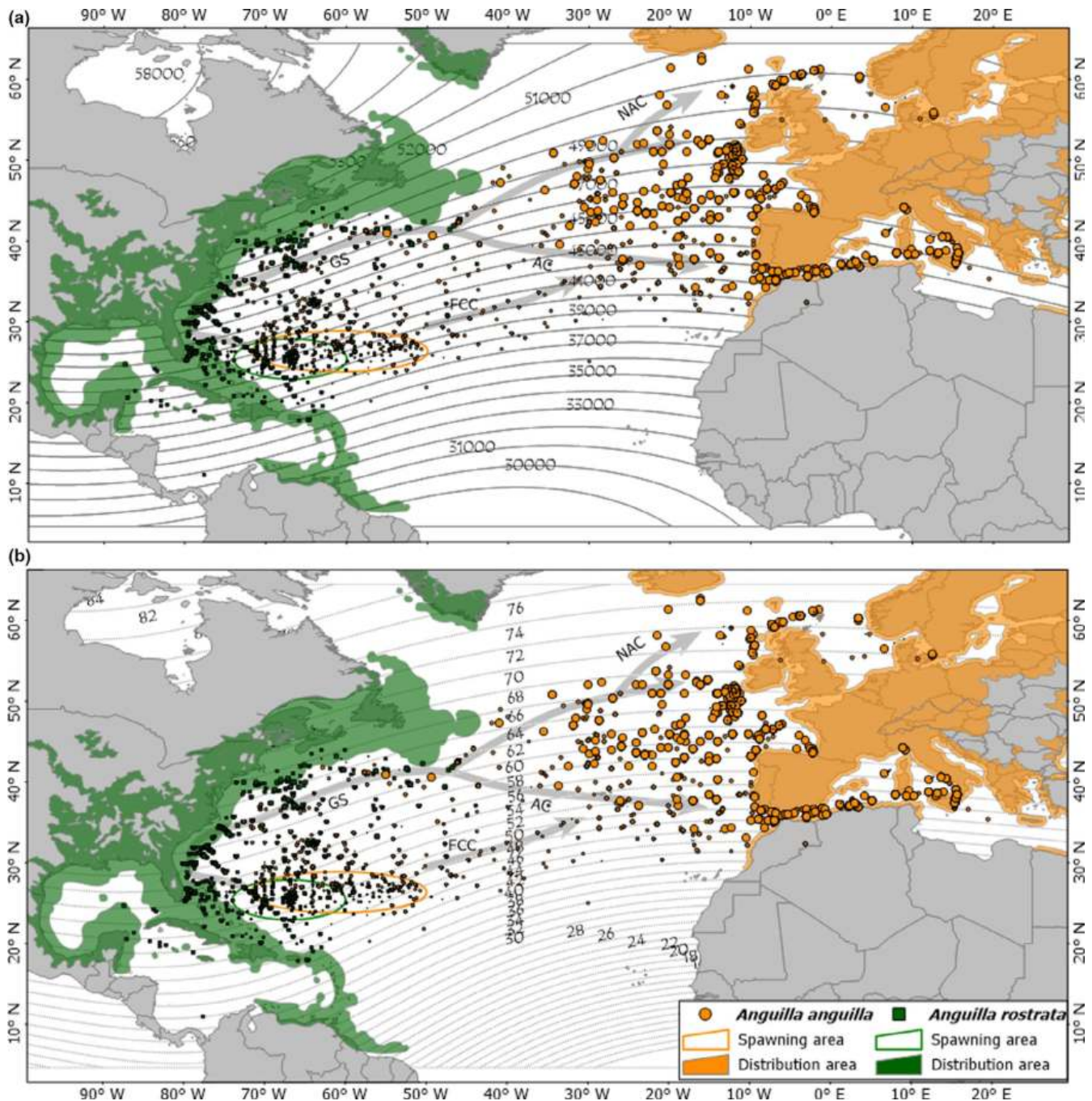


FIGURE 1 (a) Isolines of geomagnetic total intensities (contours every 500 NT) and (b) inclination (contours every 2°) calculated for the year 2014. Geographic distribution (source = IUCN) and spawning areas are represented in green and orange boxes of *Anguilla rostrata* and *A. anguilla* respectively. The dots represent collections of leptocephalus larvae (data source: ICES Eggs and Larvae database). The size of dots is proportional to the length of the larvae (3–88 mm). *A. rostrata* has been recorded in South America but its occurrence is rare (Benchetrit & McCleave, 2015). The grey arrows represent major currents in the Atlantic Ocean (AC, Azores Current; FCC, Frontal Counter Currents; GS, Gulf Stream; NAC: North Atlantic Current)

sea and start their sexual maturation and (e) the reproductive stage, about which we know very little, because sexually mature eels have never been caught alive in the wild.

We focused on five anguillid species (Figures 1–4), in the northern hemisphere (*A. anguilla*, *A. rostrata* and *A. japonica*) and in the southern hemisphere (*A. australis* and *A. dieffenbachii*). *A. rostrata*

and *A. anguilla* spawn in slightly overlapping areas of the Sargasso Sea; this is known from the distribution of catches of their larvae (McCleave et al., 1987; Miller et al., 2015; Schmidt, 1922). *A. anguilla* individuals that have embarked on their spawning migration have been tracked as far as the Azores (albeit only one individual), a location that represents approximately half of the journey to the

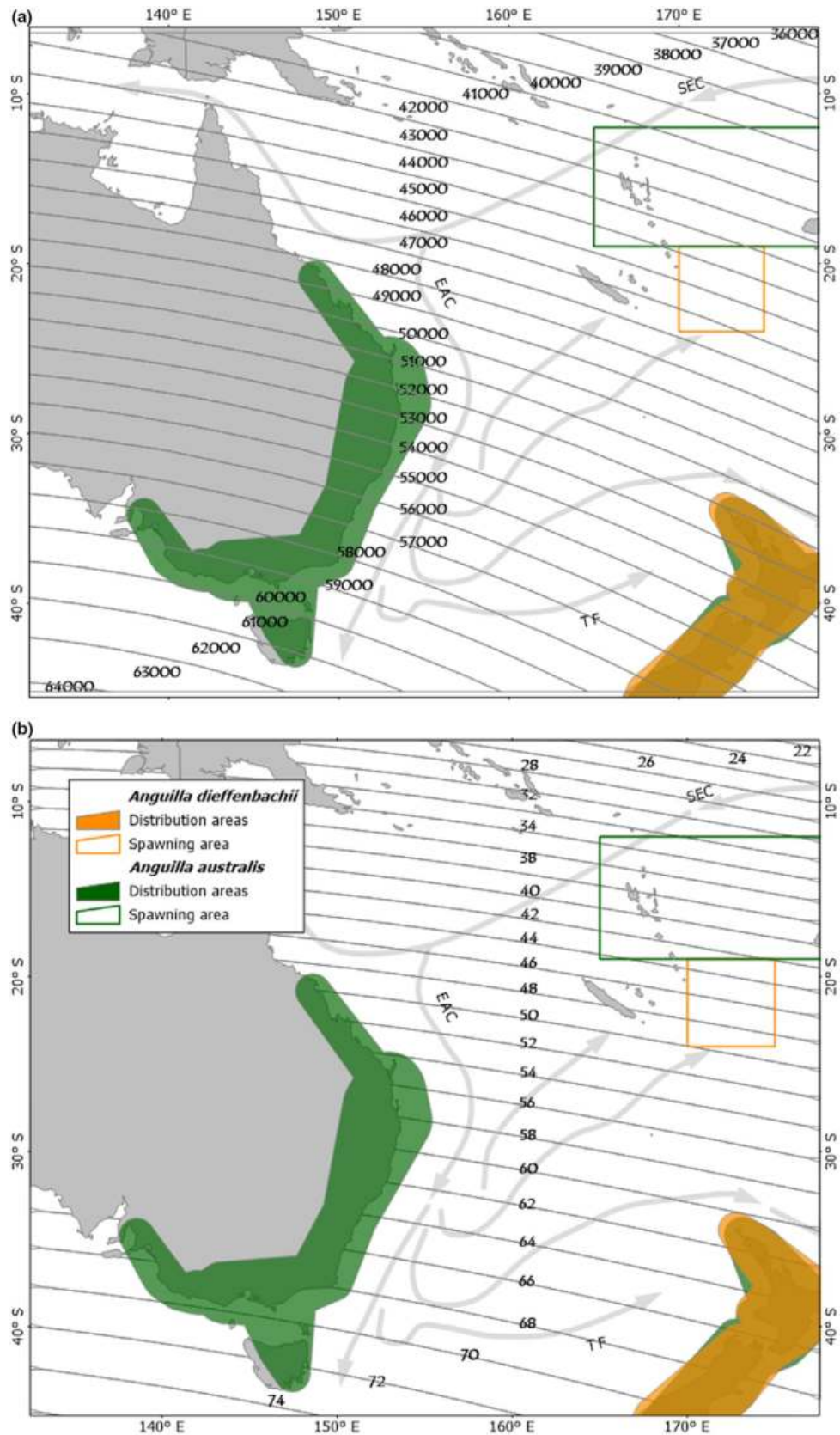


FIGURE 2 (a) Isolines of geomagnetic total intensities (contours every 1,000 nT) and (b) inclination (contours every 2°) calculated for the year 2014. Growth (source = IUCN) and spawning areas are represented in green and orange boxes for *Anguilla australis* and *A. dieffenbachii* respectively. The grey arrows represent major currents in the South Pacific (EAC, East Australian Current; SEC, South Equatorial Current; TF, Tasmanian front)

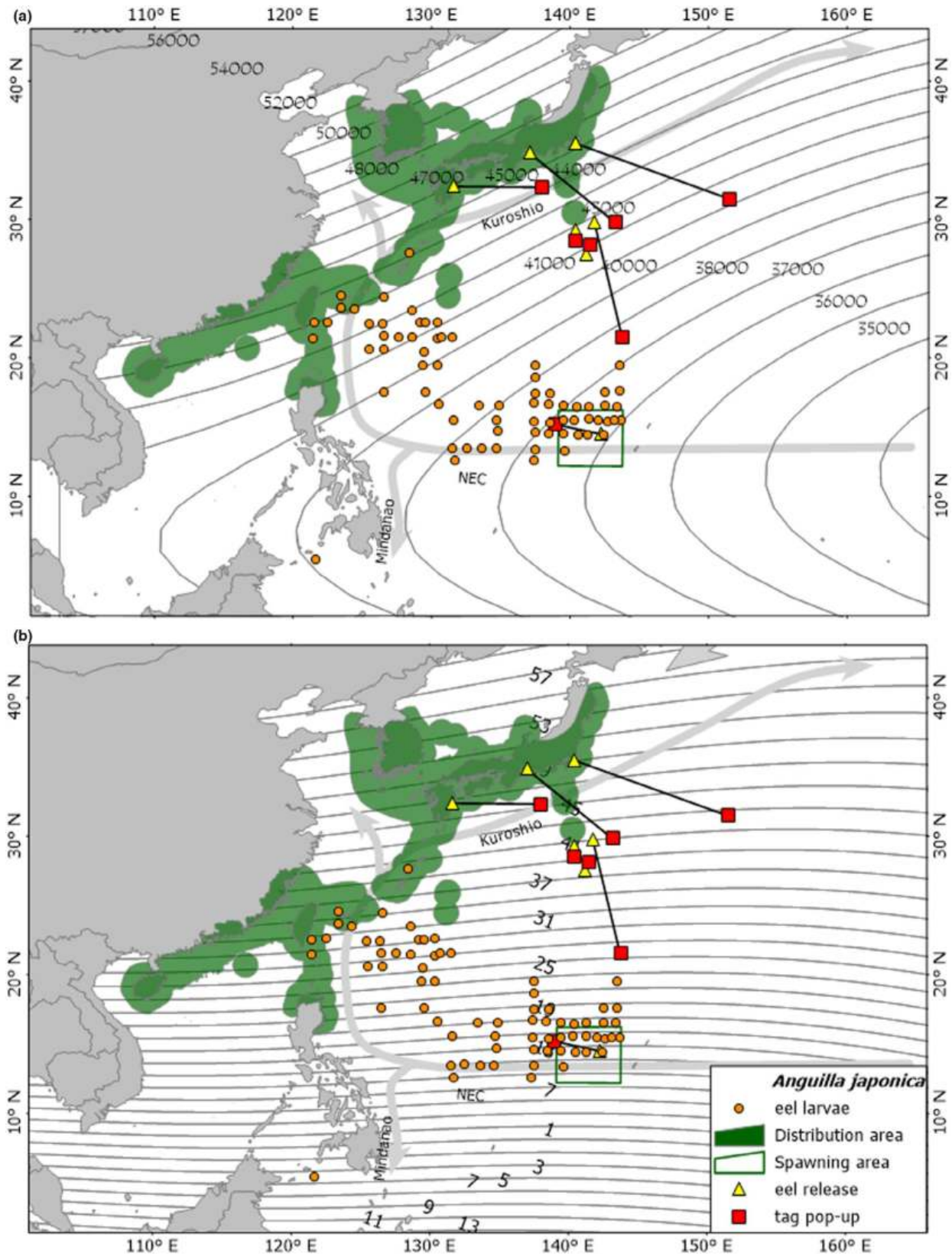


FIGURE 3 *Anguilla japonica*. (a) Isolines of geomagnetic total intensities F (contours every 1,000 nT) and (b) inclination I (contours every 2°) calculated for the year 2014. Growth (source = IUCN) and spawning (box) areas are represented in green. Leptocephalus larvae are depicted in orange (larval collection data were redrawn from Shinoda et al., 2011). The grey arrows represent major currents: Mindanao, North Equatorial (NEC) and Kuroshio currents. Japanese eel release (yellow triangles) and tag surfacing location (red square) of PSAT (pop-up satellite tag) from Higuchi et al. (2021)

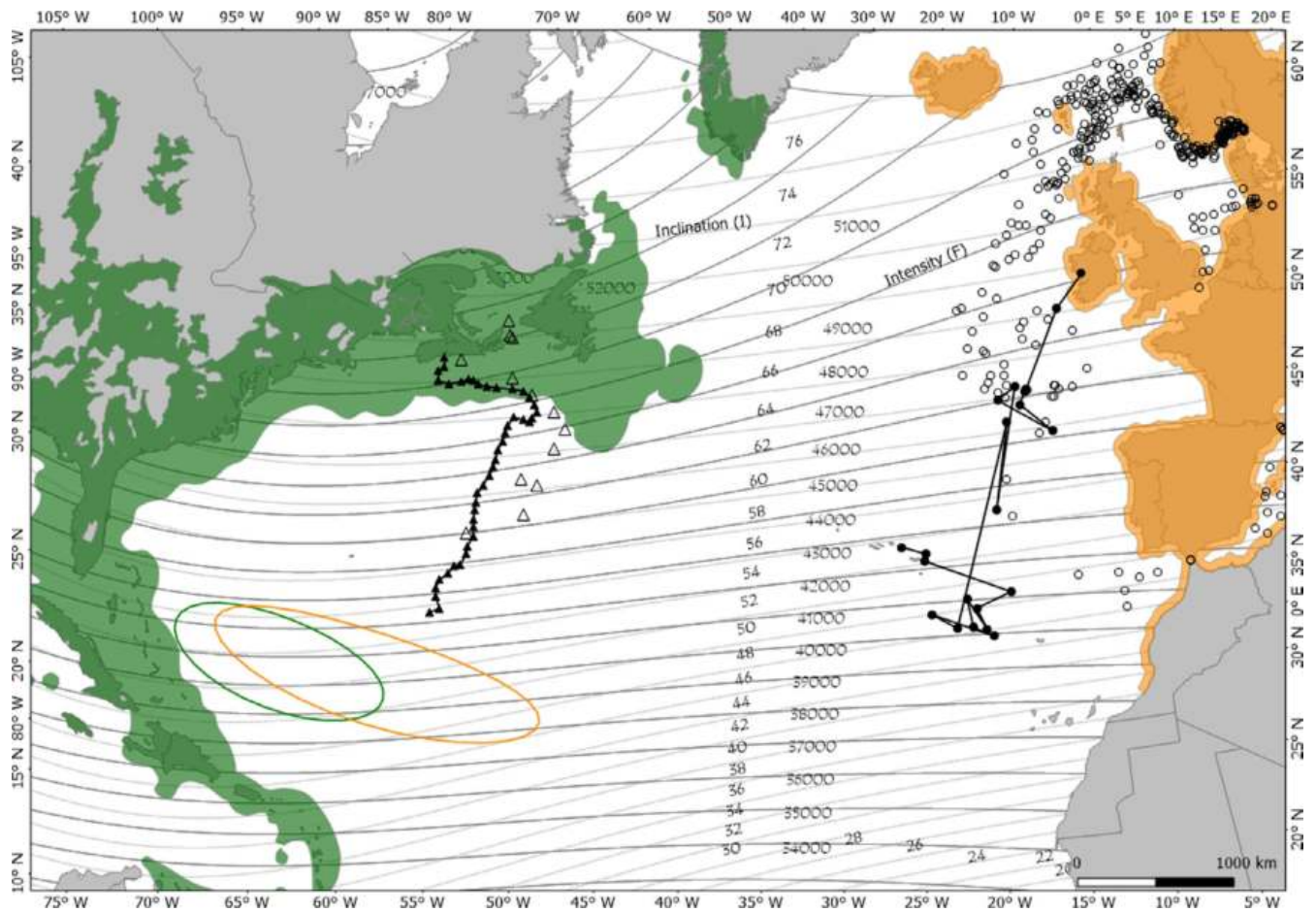


FIGURE 4 Reconstructed migrations of tagged Atlantic eels (triangles: *Anguilla rostrata*, Beguer-Pon et al., 2015; Beguer-Pon et al., 2017; circles: *A. anguilla*, Righton et al., 2016). Paths correspond to the two eels that were tracked for the longest distance. Open circles/triangles represent geolocation estimates or terminal positions—when the tag came off prematurely—of other tagged eels from Righton et al. (2016) and Beguer-Pon et al. (2017). Isolines represent geomagnetic total intensities (dark grey, contours every 1,000 nT) and inclination (light grey, contours every 2°) calculated for the year 2014. Growth (source = IUCN) and spawning areas are represented in green and orange boxes for *A. rostrata* and *A. anguilla* respectively

spawning area (Aarestrup et al., 2009; Righton et al., 2016). An individual of *A. rostrata* was tracked for 2,400 km from Canada down to the Sargasso Sea, providing the first direct evidence of the location of the Atlantic spawning area (Beguer-Pon et al., 2015).

Anguilla japonica spawns in the North Equatorial Current (NEC), west of the Mariana Islands (Tsukamoto et al., 2003). Eggs of *A. japonica* (Aoyama et al., 2014; Tsukamoto et al., 2011; Yoshinaga et al., 2011) as well as two sexually mature males (Chow et al., 2009) and two post-spawning females (Kurogi et al., 2011), were collected along the West Mariana Ridge. Several migration routes have been proposed for *A. japonica*, one that runs opposite of the Kuroshio current and one that runs on a more direct southern trajectory (Tsukamoto, 2009). However, these have not been entirely verified by tracking or collection of migrating individuals.

Seven species and subspecies of anguillid eels are present in the South Pacific region (Jellyman, 1997)—we focused on the two for which there is the most knowledge. *A. australis* is found in eastern Australia and New Zealand, while *A. dieffenbachii* is only found in New Zealand. Some anguillid leptocephali were collected south of

the Solomon Islands and provided preliminary evidence that the spawning area of *A. australis* is in the South Equatorial Current (Aoyama et al., 1999; Kuroki et al., 2008). Data from tracked eels and circulation models suggest that both species spawn in slightly overlapping areas between New Caledonia and Fiji (Jellyman & Bowen, 2009; Jellyman & Tsukamoto, 2010). Further, genetically identified larvae of *A. australis* (16–46 days) were collected south of the Solomon Islands but also 1,600 km to the east which, when taken together with the age of the larvae, suggests that the spawning area is near the Vanuatu Archipelago (Kuroki et al., 2020).

2.3 | Description of the data

2.3.1 | Geomagnetic data

To test the magnetic imprinting hypothesis, we plotted and mapped the total intensity of the geomagnetic field (F) and the inclination of its lines (I), in the distribution areas of the eel species described

above. All calculations were made using the International and Definite Geomagnetic Reference Fields (IGRF, DGRF, Thebault et al., 2015). IGRF models are models of the geomagnetic main field, modelling sources inside the earth without taking into account external sources or static crustal anomalies. Values were calculated for $\Delta\text{Long} = 1^\circ$ and $\Delta\text{lat} = 0.5^\circ$. Magnetic field values were interpolated using the kriging method to draw isolines of equal intensities/inclinations. Contour maps were created using Manifold System 8.0.

2.3.2 | Migration routes and spawning areas of eels

The spatial data for the distribution of *A. anguilla*, *A. rostrata* and *A. japonica* were obtained from the IUCN website. The distribution areas for *A. australis* and *A. dieffenbachii*, were obtained from FishBase (Froese & Pauly, 2017). Locations of spawning areas and migratory routes were obtained from the literature (Beguer-Pon et al., 2015, 2017; Higuchi et al., 2021; Kuroki et al., 2020; Miller et al., 2015; Miller & Tsukamoto, 2017; Righton et al., 2016; Shinoda et al., 2011; Takeuchi et al., 2021). Data from Pop-up Satellite Tag (PSAT) tracked *A. anguilla* silver eels on their way to the spawning area were provided by David Righton on behalf of the authors (Righton et al., 2020). The larval drift of *A. anguilla* and *A. rostrata* were described through larval collections made during surveys and were downloaded from the International Council of the Exploration of the Sea (ICES) Eggs and Larvae database. Larval collection locations of *A. japonica* were redrawn from Shinoda et al. (2011).

3 | RESULTS

3.1 | Geomagnetic gradients between growth and spawning areas

The spawning areas of *A. japonica*, *A. rostrata* and *A. anguilla* are located south of their growth area while *A. australis* and *A. dieffenbachii* spawn north of their growth area (Figures 1–3). While the geographical configurations between eels from both hemispheres are opposite, the gradients of the geomagnetic parameters are similar: The magnetic intensity values (F) and inclination (I) in the growth areas of the five species examined are always similar or higher than

in the spawning areas with little ($\Delta F < 10\,000$ nT; $\Delta I < 10^\circ$) or no overlap (Table 1, Figures 5–6).

In the case of Atlantic eels, larvae drifting with the Gulf Stream along the North American coast experience a steep gradient of increasing F and/or I (Figure 1). Further drifting towards the east results in movements roughly parallel to the F and I isolines, depending on their final destination. The routes of adult silver eels, as known from tracked individuals, retrace these magnetic gradients in the opposite direction. That is, tracked eels followed a steep gradient of decreasing F and/or I almost perpendicular to the isolines (Figure 4). Tracks of both species were parallel to each other, keeping a heading of approximately 200° for *A. anguilla* and 190° for *A. rostrata*. *A. anguilla* changed its course at $F = 41\,000$ nT, $I = 49^\circ$ and the last detections were at isolines $F = 43\,000$ nT, $I = 54^\circ$ for both species. Following either one of these “target isolines” by maintaining a compass heading of approximately 260° would lead the adult eels to the spawning area.

The situation for *A. australis* and *A. dieffenbachii* in the southern hemisphere is comparable to that of *A. rostrata* and *A. anguilla* regarding both magnetic components and oceanic circulation. Larvae drifting with the South Equatorial Current and East Australian Current experience gradients of increasing F and/or I at the beginning of the drift period which level off as larvae drift east to reach New Zealand in the same manner as in the Atlantic Ocean for *A. anguilla* (Figures 1–2). Migrating adults that swim towards decreasing F and/or I until target isolines $F = 43\,000$ nT, $I = 40^\circ$ (for *A. australis*) and $F = 46\,000$ nT, $I = 46^\circ$ (for *A. dieffenbachii*), and follow these isolines, would arrive at their spawning area.

The configuration is slightly different for *A. japonica* as F and I isolines run perpendicular to one another in the spawning area. However, larvae drifting with the North Equatorial Current (NEC) and Kuroshio current still experience increasing F and I (Figure 3). The migratory routes of adult eels, as they are known from PSAT studies, also follow the reverse gradient moving towards lower F and I (Figure 3). Their trajectories were slightly deviated towards the south east. Tags were released before eels reached the spawning area (or the spawning area isolines), but if eels had kept these headings they would have arrived in the spawning area by shifting their orientation by approximately 90° to the right once they had reached the target isolines (Figure 3).

TABLE 1 Characteristics of the distribution of magnetic total intensity (F) and inclination (I) values at the spawning areas of five species of anguillid eels (*Anguilla* spp.). Values were calculated for the year 2014

| Species | I ($^\circ$) (min–max) | | | F (nT) (min–max) | | |
|-------------------------|----------------------------|------------|---------|--------------------|---------------|---------|
| | Growth area | Spawning | Overlap | Growth area | Spawning | Overlap |
| <i>A. anguilla</i> | 46–77 | 42–56 | 10 | 39,000–53,000 | 37,847–44,949 | 5,949 |
| <i>A. rostrata</i> | 46–74 | 46–56 | 10 | 37,000–53,000 | 38,971–44,841 | 9,758 |
| <i>A. japonica</i> | 21–55 | 3–16 | 0 | 41,000–48,000 | 36,513–38,001 | 0 |
| <i>A. australis</i> | 48–72 | –29 to –44 | 0 | 49,000–61,000 | 39,120–45,773 | 0 |
| <i>A. dieffenbachii</i> | 60–70 | –42 to –50 | 0 | 53,000–59,000 | 43,772–47,790 | 0 |

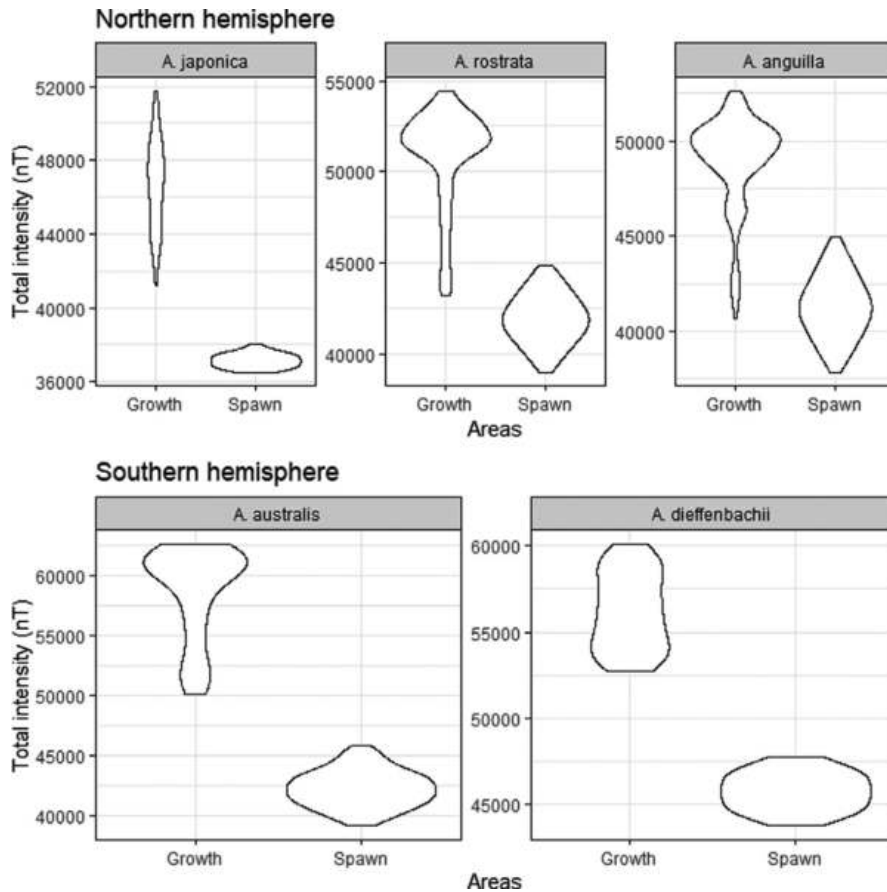


FIGURE 5 Total magnetic intensities (F , nT) modelled in growth areas and spawning areas of five different species of anguillid eels. In the Northern hemisphere (top figures): *Anguilla anguilla*, *A. japonica* and *A. rostrata*. In the Southern hemisphere: *A. australis* and *A. dieffenbachii*

For all species, the spawning areas are located at the same magnetic isoline as the southern (northern in the southern hemisphere) limits of the species distribution (Figures 1–3). For example, *A. anguilla* occurrence extends down to Morocco which has the same magnetic intensity/inclination as the south-eastern limit of the spawning area (Figure 1). For the *A. rostrata*, the magnetic isolines running through the spawning area, end up in the Dominican Republic, which roughly corresponds to the southern limit of *A. rostrata* distribution—at least to a limit below which almost no larvae have been collected. The configurations of the Gulf of Mexico and of the Mediterranean Sea are analogous: although they are at different latitudes, they display similar magnetic values. The F and I isolines at the Strait of Gibraltar correspond exactly to the lower distribution limit of *A. rostrata* in Cuba ($F = 41\,000$ nT and $I = 49^\circ$). Eels hatching in the most south eastern corner of the spawning area would also experience increasing F and I while drifting towards either the Gulf of Mexico or the Mediterranean.

3.2 | Secular variation

When considering a mean age at silvering of 20 years and a hatching date in 1900 (Atlantic eels), ΔF in the Sargasso Sea is $<1,000$ nT, $\Delta I < 1.3^\circ$ (Figure 7). Between 1900 and 1920, this corresponds to a

spatial displacement of the geomagnetic features of the spawning site of about 200–500 km (when using F) and about 130 km (when using I). For *A. japonica*, with a mean age at silvering of 10 years, ΔF in the North Pacific is <100 nT and $\Delta I < 0.3^\circ$ which corresponds to maximum displacements of 20–50 km and 30 km respectively using F and I .

4 | DISCUSSION

4.1 | A general mechanism for navigation of migrating temperate anguillid eels

The migratory routes of five species of anguillid eels (*A. anguilla*, *A. rostrata*, *A. japonica*, *A. australis* and *A. dieffenbachii*) are consistent with the use of the geomagnetic field as a navigational cue to reach their spawning area. The mechanism that we propose is possible using only one component, either magnetic intensity (F) or inclination (I). Although, the use of I is less likely for reasons that are discussed later, we cannot completely exclude it until we obtain further evidence of the actual migratory route of silver eels.

The general long-distance navigation mechanism for anguillid eels can be described in five steps, for which we provide additional support below. No animal is believed to rely solely on geomagnetic cues for orientation (Clites & Pierce, 2017; Mouritsen, 2018) and our

FIGURE 6 Inclination angles (I°) modelled in growth areas and spawning sites of five different species of anguillid eels. In the Northern hemisphere (top figures): *Anguilla anguilla*, *Anguilla japonica* and *A. rostrata*. In the Southern hemisphere: *A. australis* and *A. dieffenbachii*

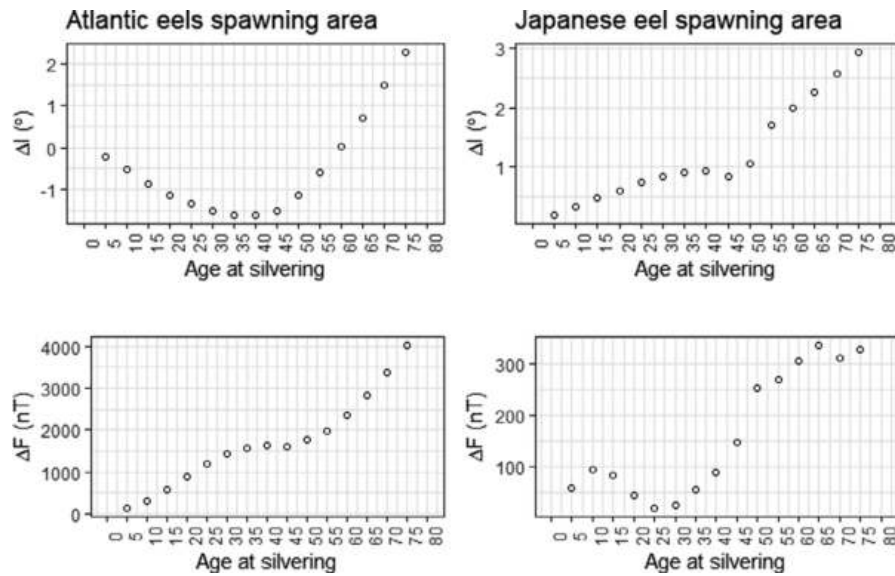
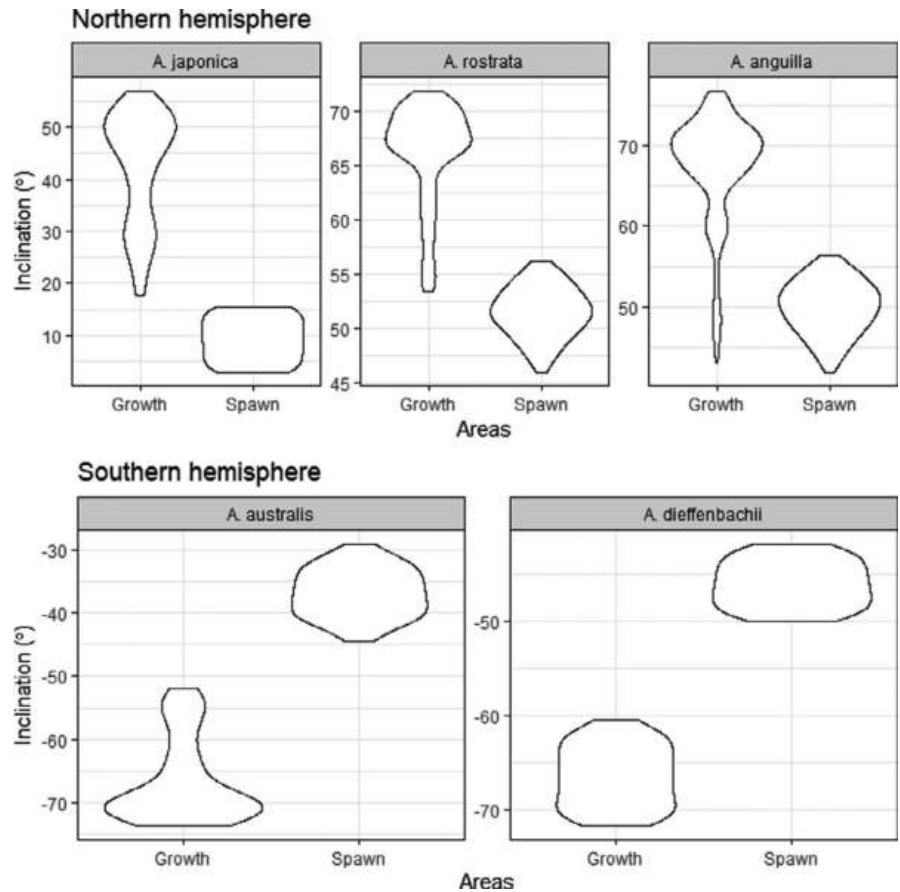


FIGURE 7 Differences in magnetic parameters (total intensity and inclination) that a silver eel would experience upon return to the spawning area where it hatched according to its age. Values represent the difference in total magnetic intensity (F) and inclination (I) at the spawning area between of a hypothetical eel hatching in 1900 and spawning at different ages between 5 and 80 years old (age at silversing). $\Delta F = F_{\text{hatch}} - F_{\text{spawn}}$ and each triangle the difference $\Delta I = I_{\text{hatch}} - I_{\text{spawn}}$. Values were calculated at 63°W , 25°N (left panel, European (*Anguilla anguilla*) and American eel (*A. rostrata*) spawning area) and at 140°E , 12°N (right panel, Japanese eel (*A. japonica*) spawning area)

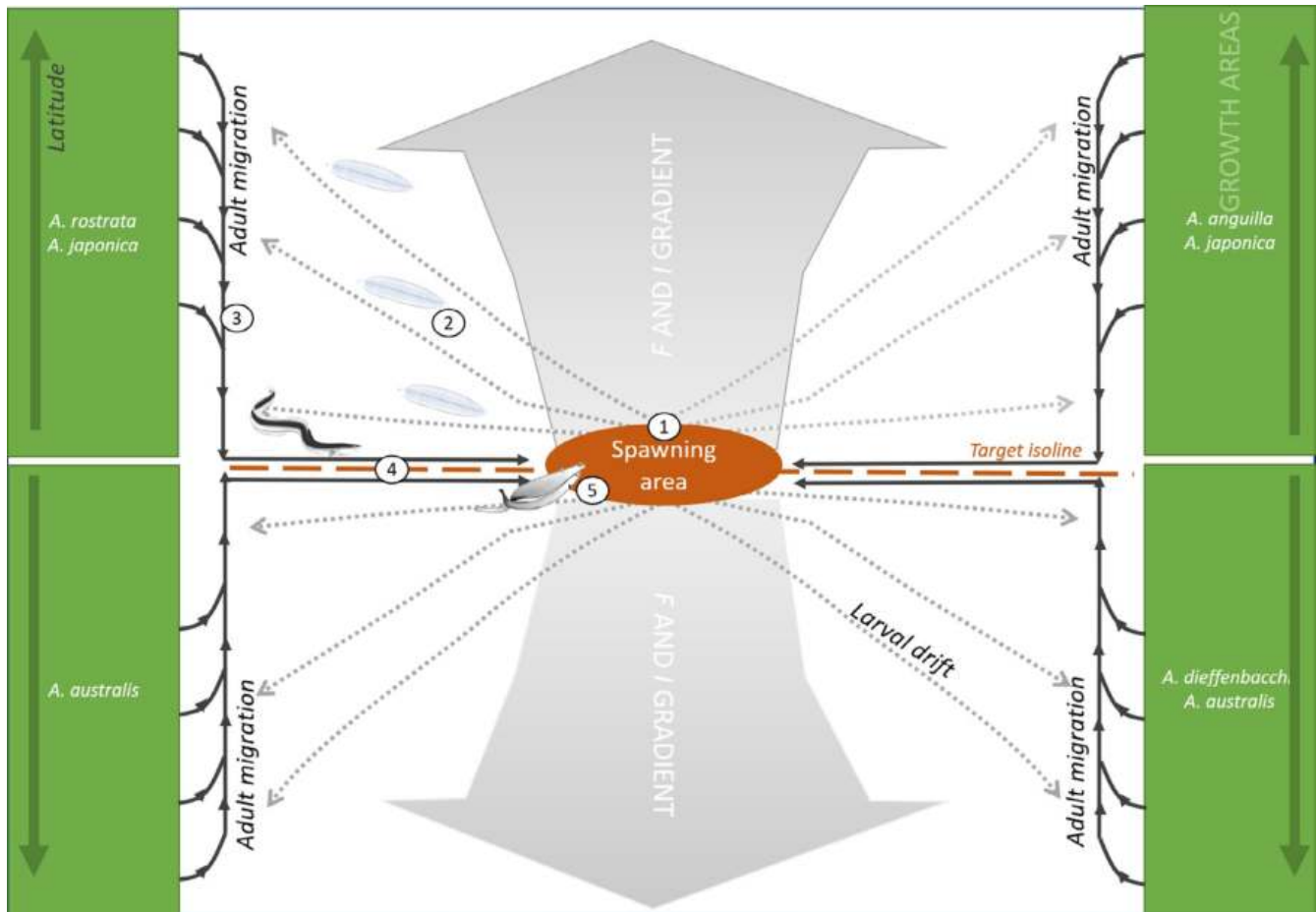


FIGURE 8 General mechanism for the navigation of temperate anguillid eels (*Anguilla* sp.) using the geomagnetic field (F : total intensity, I : inclination). Step 1: The target isoline (either F or I) is imprinted at a very early larval stage; step 2: Leptocephalus larvae imprint the F or I gradient during their larval drift towards the continent; step 3: Adult eels migrate along the reversed F or I gradient; step 4: Adult eels reach the target imprinted isoline and orient according to a compass heading to remain on the isoline; step 5: Physiological (end of sexual maturation) and olfactory cues (coming from conspecifics) provide the stop signal. Eels congregate and spawn. Each quadrant repeats the 5 steps in the four possible geographical configurations between growth and spawning areas. Light dashed arrows represent the leptocephalus drift towards the continent. Darker arrows depict the reproductive migration

model, although it relies mainly on magnetoreception, also includes physiological cues which are discussed below. The proposed mechanism is conceptualized in Figure 8 and is described as follows:

1. Larvae hatch and imprint the local intensity or inclination (F_{hatch} or I_{hatch}).
2. Larvae drift towards their growth area and register the F (or I) gradient that they experience along the way until they reach their destination.
3. Years later, at the time of the spawning migration, adults follow the reverse magnetic gradient that they have imprinted as juveniles, which, as far as the species examined are concerned, corresponds to decreasing F (or I).
4. Adults reach the target isoline, F_{hatch} (or I_{hatch}) and keep a compass heading to stay on the target isoline.
5. As the entire eel spawning population congregates towards the target isoline, individuals become fully sexually mature and are

ready for spawning. The timing of sexual maturation likely determines the geographic location along the longitudinal axis which may vary slightly from year to year.

4.2 | Migratory steps 1 and 2: Imprinting and the magnetic map hypothesis

Silver (adult) eels take different oceanic/geographic routes than the ones taken as larvae, thus they can be considered as a first-time migrant. The only way for a first time-migrant to reach its target is to inherit the information (Mouritsen, 2018). In the case of eels, pre-programmed navigation seems unlikely given secular variation. We show that the “magnetic routes” of larvae and adults are alike and therefore that adult eels have had the opportunity to learn or imprint the magnetic information necessary for the return journey.

These geomagnetic patterns are consistent between species and are also consistent with the magnetic imprinting hypothesis (Figures 1–6). Magnetic total intensity (F) and inclination (I) between growth and spawning areas are almost identical between all five species examined (*A. anguilla*, *A. rostrata*, *A. japonica*, *A. australis* and *A. di-ffenbachii*). Drifting larvae always experience increasing magnetic inclination (I) and total intensity (F). The return routes of adults in the open ocean, as far as they are known, correspond to the same gradients but in the opposite direction. By imprinting either F or I target isolines (at hatching), as well as the steepness of the gradients experienced as larvae (during the drift), eels can home back to the spawning area by retracing these magnetic patterns later as adults. The range of the imprinted magnetic values (either F or I) may vary depending on the extent of the larval dispersal. For example, a larva drifting between the Sargasso Sea and the Mediterranean or to the Gulf of Mexico will experience a smaller range of magnetic values compared to larvae recruiting to Norway or Canada. Their imprinting experience may define the range of variation of their magnetosensory system for later use during the spawning migration. Such a calibration system was observed in the pigeon (*Columba livia*, Columbidae), and the nematode (*Caenorhabditis elegans*, Rhabditidae), for which the neuronal response became saturated when exposed to intensities larger than the geomagnetic field (Vidal-Gadea et al., 2015; Wu & Dickman, 2012). Further indirect evidence for imprinting of geomagnetic components comes from several observations. Steelhead trout (*Oncorhynchus mykiss*, Salmonidae) which, when raised under an unnatural magnetic field failed to orient while those raised under natural magnetic conditions did (Putman, Scanlan, et al., 2014). Stocked eels that were translocated from France to Sweden as juveniles were not able to find their way out of the Baltic sea when they reached the silver stage (Westin, 1990). Instead, they continued in a south-westerly direction—as they would have oriented had they been departing from France—and were found in the same area more than 4 years later. Unusual behaviour of silver eels (stocked as juveniles) was also observed in Estonia, whereby 21% returned to their river after an attempted migration (Tambets et al., 2021). One fish was recaptured in Finland and only 13% were detected exiting the Baltic. Similarly, translocated brown trout (*Salmo trutta*, Salmonidae) lost their ability to home to their native river when deprived of environmental cues during their transport out to the sea (Jonsson & Jonsson, 2021).

4.3 | Migratory steps 3 and 4: «Aiming off»

As silver eels leave continental waters and reach the open ocean, cues such as salinity or odour plumes from rivers, disappear. Beyond continental shelves, migrating eels seem to follow decreasing magnetic intensities (F) and/or inclination (I) until they have reached the isolines that correspond to their spawning area. This is supported by data from tagged *A. anguilla* which were tracked for at least half of the spawning migration (Righton et al., 2016). Interestingly, eels

did not take the shortest way back to the Sargasso Sea (Aarestrup et al., 2009; Righton et al., 2016), but instead first headed south along a gradient of magnetic intensities (or inclinations) that is similar to the one experienced at the beginning of their larval drift, along the north American coast in the Gulf Stream (Figures 1 and 4). The eel with the longest track changed its course around the magnetic isoline (Figure 4, $F = 41\,000$ nT, $I = 49^\circ$) that runs through the spawning area in the Sargasso Sea. Eels released in the Mediterranean, and thus already at ($F = 41\,000$ nT, $I = 49^\circ$), followed a western heading towards the Azores (Amilhat et al., 2016). The tracks of more than 80 eels were reconstructed (Figure 4), and although many were predated upon, all trajectories converged on the Azores region (Righton et al., 2016). Once there, eels would presumably maintain a western heading towards the spawning area. The tracks of tagged *A. japonica* were also consistent with our model (Higuchi et al., 2021). Eels moved along decreasing F and I gradients at least until their tags were released. Eels did not swim directly to the spawning area but swam southeast of the spawning area. The authors hypothesized that eels would later move southwest with the flow of Kuroshio recirculation or the subtropical gyre. Thus, “aiming off” seems to occur in both species. This navigation technique involves aiming away from the destination but instead heading towards a “line feature” such as a stream (here a magnetic isoline) some distance to the left or to the right of the target. Steps 3 and 4 of our model, as well as observations of tagged eels, are consistent with this efficient strategy, which has at least two advantages: (1) It is the most efficient strategy to find conspecifics. Rather than heading straight for a target, beginning at one end and keeping a constant heading will increase the chance of meeting conspecifics along the way. *A. anguilla* coming from—for example, Norway—have a better chance of meeting eels from Morocco along a narrow latitudinal band ($F = 41\,000$ nT, $I = 49^\circ$) than at a target point. This is consistent with the panmictic nature of this species. (2) This navigational strategy also allows for the use of other orientation cues such as olfaction (see the discussion of olfactory cues). Finally, the geomagnetic patterns along the migratory route are compatible with an “aiming off” strategy (descending F and I gradients then following the axis of the isoline) and this is demonstrated in the trajectory of tagged eels.

Eels likely use compass orientation as they travel towards decreasing F and I , while periodically taking “measurements” until they reach the target isoline where they switch compass heading. Compass sense has been reported in the continental life stages of the *A. anguilla* (Cresci et al., 2017; Durif et al., 2013). Such a mechanism, which consists of a sequence of compass headings changing at specific magnetic field values, is well documented in birds (Åkesson & Helm, 2020; Kiepenheuer, 1984). For example, under laboratory conditions pied flycatchers (*Ficedula hypoleuca*, Muscicapidae) shift compass orientation when exposed to changes in magnetic field intensity corresponding to those encountered during their natural migration (Beck & Wiltschko, 1982). During the experiments, the shifts in heading occurred at the same time as for conspecifics during their natural migration.

4.4 | Migratory step 5: The end of the journey

Our model does not require that eels possess navigational abilities along the longitudinal axis, but instead relies on a strategy that will allow for eels from all of the distribution area to congregate. The spawning area as we know it, at least for the Atlantic eels, represents a very large area. Research cruises carried out in 2014 collected larvae ≤ 20 days old across a longitudinal range of about 2000 km (Miller et al., 2019). Furthermore, at the time of spawning, hundreds of millions—in some years possibly billions—of eels migrate from Europe every year (ICES, 2020). Given this, a precise navigation system to a specific target is not needed. Rather a common mechanism to follow the same route and meet along this route would be required. As for flycatchers (see above discussion), eels may rely on an endogenous time program coupled with magnetic parameters of specific locations throughout their migration and as they become sexually mature. As in several other fish species, eels undergo extreme morphological and physiological changes during the last steps of their sexual maturation. Bodies of females become swollen (the percentage of eggs relative to body mass can reach 50%), they undergo osteoporosis and the energy stores in both sexes are depleted (Durif et al., 2006; Fontaine et al., 1964; Sbaihi et al., 2009). In other words, at full sexual maturation, eels are inefficient swimmers that are physically unable to continue swimming long distances. In fact, they die soon after ovulation/spermiation (Chow et al., 2009).

An additional cue that would reinforce orientation throughout the reproductive migration is odour. Odour plumes, such as pheromones left by conspecifics, may provide a trail guiding eels, especially during the last part of the journey up to the Azores current. In Salmonids, eggs and ovarian fluids produce odours that guide adults to the breeding sites (Dittman & Quinn, 2020). In eels, olfaction is important throughout their life cycle. Glass eels are attracted by the smell of their conspecifics (Cresci, 2020; McCleave & Jellyman, 2002; Schmucker et al., 2016). Silver eels use olfaction during their estuarine migration and olfactory cues trigger migration into rivers (Barbin et al., 1998; Durif et al., 2008). As progressively more and more mature individuals pass along the same route, they will leave olfactory signals. Tracked eels exhibited diel vertical migrations (Aarestrup et al., 2009); this would be an effective way to spread the olfactory tracks through the water column. In the laboratory, sexually mature eels (artificially induced) showed higher gene expression of receptors related to olfaction, which suggests a role of olfaction in reproduction and possibly also in orientation (Churcher et al., 2015).

4.5 | Use of inclination (I) and/or total intensity (F) in the navigation of eels

We examined the patterns of I and F since they are both correlated with latitude and are measurable components of the magnetic field. In most configurations, the gradients were parallel and, therefore, whichever parameter, F or I , is used by eels does not change the

overall mechanism. Our analysis of the potential effect of secular variation suggests that I is the best candidate for magnetic navigation since maximum potential displacement ($\Delta I_{\max} = 130$ km) was lower than for F ($\Delta F_{\max} = 500$ km). However, comparing patterns of I and F between species favoured F . Indeed, we found that F patterns were very similar across species, while I patterns were different near the *A. japonica* spawning area since the isolines of F and I run perpendicular to each other (Figure 3). At present, it is not possible to determine which component is more likely to be used—or if both are used—since we have very little knowledge on the routes of migrating adults of *A. japonica*. If adult *A. japonica* were to adopt the same strategy as the other species, that is, following a decreasing gradient and then following an isoline, then patterns of F would match. Silver eels would follow a south-easterly heading until isoline $\sim F = 36\,000$ nT, after which they would keep a constant heading in a south-westerly direction until they reached the spawning area (Figure 3).

From a physics point of view, one fundamental difference between magnetic intensity and inclination is that F is a scalar value while I is an angle. Thus, measuring variations in I is a much more complex feat for an eel than measuring total intensity (F). As one approaches the equator (where I is equal to zero), the signal-to-noise ratio will deteriorate much more for I than for F . Another advantage of F is that while it also decreases towards the equator, it will not be zero at the equator and (for Thebault et al., 2015) will have values between 30,000 and 40,000 nT (while it is around 55,000 nT at the poles), depending on the location along the equator. Further, while measurement of F (scalar) is independent of one's position in space, I being an angle is measured relative to the horizontal plane or to a gravitational reference system which makes it a challenge underwater. However, loggerhead sea turtles (*Caretta*, Cheloniidae) and eastern red-spotted newts (*Notophthalmus viridescens*, Salamandridae) seem to accomplish this as they can detect differences in I as small as $2\text{--}3^\circ$ (Fischer et al., 2001; Lohmann & Lohmann, 1994). Overall, our analyses and the physics, appear to make F more likely to be used than I .

4.6 | Geomagnetic secular variations

For animals to use a magnetic map requires that they are highly sensitive to gradients, and that they have a system/mechanism to handle static magnetic anomalies (due to the magnetized sea floor), short term variations (e.g. magnetic daily variations) and secular variation. Historically, the magnetic poles have been drifting between 10 and 20 km annually, but an acceleration (about 50 km/year) began around 1990 in the northern hemisphere (Thebault et al., 2015). Adaptations for maintaining migratory behaviour must be capable of handling fluctuations on these time-scales and this is also an argument against a genetically programmed navigational target (Courtillot et al., 1997).

There are several ways an organism can deal with secular variation. Long-term temporal measurements might be factored out by regular measurements of the magnetic field at one specific location (Freake

et al., 2006). In other words, an eel may “register” the changes over its life cycle in its current location and adjust the target coordinates that will be used during the spawning migration. However, this seems unlikely given the long migration distances and the fact that the magnitude of changes in the field varies across the Earth's surface.

Another way to mitigate the displacement due to secular variation is to imprint the target destination at an early stage of the life cycle rather than transmitting it to offspring (genetically programmed) (Lohmann et al., 2008; Putman, Scanlan, et al., 2014; Putman, Scanlan, et al., 2014). This is supported by our findings (see ‘Imprinting and the magnetic map hypothesis: steps 1 and 2’). Yet, in such long-lived species as anguillid eels, there can still be an effect of secular variation over the course of an eel's lifecycle. Accounting for the age of silver *A. anguilla*, we calculated that the maximum geographic displacement that would result from secular variation in the Atlantic would be approximately 300 km if magnetoreception was based on *F* and 100 km based on *I*. Displacements for *A. japonica* silver individuals would be around 30 km. These are very rough estimates which also depend on the years chosen, but they give a reasonable order of magnitude which could be overcome through olfactory cues given the extent of the spawning migration (hundreds of millions of eels per year, ICES WGEEL (2020), estimates for *A. anguilla*). Moreover, waves of migrating silver eels are synchronized according to latitude: eels in the north leave earlier than eels in the south as they have more distance to cover. As explained previously, age at migration decreases with latitude (Durif et al., 2009; Jessop, 2010; Vøllestad, 1992). Females and/or males from the southern part of the distribution may migrate after only 2 years, thus reducing the offset in the imprinted magnetic components (ΔI and ΔF) to a negligible level, with $\Delta I \approx 0.2^\circ$ and $\Delta F \approx 50$ nT (Figure 7). This corresponds to a displacement of 10 to a maximum of 20 km which can easily be resolved using olfactory cues given the total annual number of spawners. Eels from the southern part of the distribution probably arrive first and will provide essential olfactory cues in the form of an odour plume conveyed by the Azores current (which flows from the west) that will guide the rest of the spawners.

4.7 | Perspectives

Anguillid eels are fascinating in the sense that they are present in both hemispheres and that different species share very similar biological characteristics and life-histories (catadromy, long-distance migrations and long lifecycle). It seems reasonable that temperate eels would use the same navigational strategy to home to their spawning area having evolved from a common ancestor (Inoue et al., 2010). Indeed, the mechanisms described in this study for finding the spawning area—based on imprinting geomagnetic gradients, retracing them later as adults, “aiming off” using the imprinted target isoline and compass orientation—fit with the geomagnetic patterns present in the distribution area for all of the species examined and the migratory routes of these eels as they are currently known.

The model that we have described only applies to the oceanic part of their migration and does not address the coastal part of the journey where other sensory cues are available from continental waters (salinity gradients and odour plumes from rivers). While very early life stages of eels probably do not orient actively, older larvae that have reached the continental shelf and which ultimately metamorphose into glass eels, have become stronger and are likely capable of orientation and sensing other cues which would guide them towards freshwater habitats (Chang et al., 2018; Cresci et al., 2021; Rypina et al., 2014).

If our hypothesis is correct and eels need to imprint their migratory route, then current stocking programs—in which juvenile eels are translocated to eel-depleted areas—are unlikely to contribute to the recovery of the population. Fishing for glass eels is currently allowed in many EU countries under the condition that 50% of the catch is dedicated to stocking. Glass eels are usually displaced from southern Europe to the Baltic Sea. When this is done, translocated glass eels are not exposed to the magnetic cues needed for successful navigation back to the spawning area. In recognition of this weakness in translocation programmes, reintroduction of brown trout now includes towing juveniles in the sea to allow them to learn environmental cues during their seaward journey. This increases their chances of returning to their home river (Jonsson & Jonsson, 2021). This is something that should also be considered for eels and other species with analogous life histories that include long-distance migrations.

Further knowledge on the migratory routes of adults, as well as the location of spawning areas, will allow our hypotheses to be tested more comprehensively. Until then, magnetic navigational cues, as described here, could be incorporated into biophysical models to help guide future expeditions in search of eel spawning areas and provide more knowledge on the spawning migration of anguillid eels in a manner analogous to what has been applied to assess how a lunar compass aids glass eel orientation (Cresci et al., 2021).

Finally, the migration orientation mechanism proposed here implies that the location of the spawning area of *A. anguilla* is much larger than had been thought and that it shifts as a result of secular variation. That may partly explain why it has proven difficult—despite >100 years of effort—to locate it.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Caroline Durif: Conceptualization, Methodology, Investigation, Visualization, Writing—Original draft, Funding acquisition. Hans Hagen Stockhausen: Conceptualization, Investigation, Methodology, Writing—Review and editing, Visualization. Anne Berit Skiftesvik:

Conceptualization, Writing—Review and editing, Funding acquisition. Alessandro Cresci: Conceptualization, Visualization, Writing—Review and editing. Daniel Nyqvist: Conceptualization, Writing—Review and editing. Howard Browman: Conceptualization, Writing—Review and editing, Funding acquisition.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NMDC at <http://doi.org/10.21335/NMDC-1870239141>, reference number NMDC-1870239141.

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