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Whether European eel leptocephali use the Earth's magnetic field to guide their migration remains an open question

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European eels (*Anguilla anguilla*) migrate between the southwestern Sargasso Sea and the European and Mediterranean coasts. In a recent paper in *Current Biology*, Naisbett-Jones *et al.* [1] claim to “provide the first evidence that they [eels] derive positional information from the Earth's magnetic field” and that this information guides their migration. The evidence reported by Naisbett-Jones *et al.* [1] in support of this conclusion was derived from eels collected in the Severn River (UK), approximately 50 km upstream of the estuary (i.e. not “in the Severn Estuary” as stated by the authors). Eels collected this far into rivers are benthic and fully adapted to freshwater; that is, they are late-stage glass eels (~ 2 years old), not the pelagic leptocephalus (larval) life stage that actually undertakes the trans-Atlantic migration. The entire interpretive framework for the Naisbett-Jones *et al.* [1] study rests on the assumption that the behaviour of these late-stage freshwater glass eels, and their responses to magnetic fields, can be used as a proxy for the responses of eel leptocephali. The authors present no evidence in support of this key assumption.

The eel leptocephalus is a true larval form. It has completely different morphology, musculature, organ systems and behaviour from the other eel life-stages [2]. These differences are so striking that the leptocephalus larva was long believed to be a different species (*Leptocephalus brevirostris*). Late-stage glass eels display very specific behavioral patterns focused on their upstream migration in freshwater [3]. Their behavioural patterns and responses are adapted to a distinct set (and range) of environmental factors different from those of leptocephali. Thus, it is unrealistic to expect the eels studied by the authors to behave in the same way as leptocephali.

The authors' interpretations imply an additional assumption: that exposure to magnetic fields associated with the Sargasso Sea trick late-stage glass eels into thinking that they are back in the middle of the Atlantic Ocean when they are actually inland, in freshwater and at a higher temperature. We argue that a more parsimonious explanation is that the contradictory mixture of inappropriate physical and geomagnetic signals confused the late-stage glass eels, thereby explaining the “substantial variation in orientation among individuals” [1].

In addition to the unsubstantiated assumptions made about equivalence of life-stages, the study has several other critical flaws. The experiments of Naisbett-Jones *et al.* [1] were conducted in orientation arenas filled with 15 cm of freshwater, at 26°C, i.e. conditions very different from what eel leptocephali would encounter during their trans-Atlantic migration. During the test, glass eels were observed escaping from a central compartment into one of twelve peripheral chambers — this was the behaviour that was used by the authors to indicate orientation. Importantly, to move from the central compartment to one of the chambers, the eel had to crawl out of the water. Crawling out of the water is not something that a pelagic leptocephalus larva would ever do. For these reasons, we contend that the observations made by the authors to assess orientation cannot be

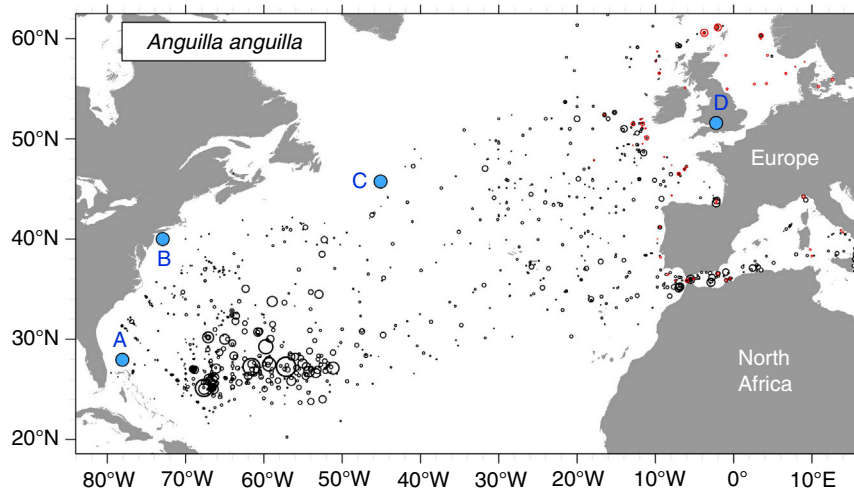


Figure 1. Historical collection locations and abundance of leptocephali. Locations where European eel (*Anguilla anguilla*) leptocephali have been collected according to the most recent database [4]. Letters A–D: values of magnetic fields used in the study by Naisbett *et al.* [1], corresponding to (A) the Sargasso Sea, (B) the northwest Atlantic, (C) the northern mid-Atlantic, and (D) the ambient field in Wales, United Kingdom. Size of circles is proportional to the number of samples collected.

used — without caveat — to make inferences about the behavior of leptocephali.

The magnetic fields to which late-stage glass eels were exposed in the experiments of Naisbett-Jones *et al.* [1] were selected to simulate those encountered by eel leptocephali at locations along their migration route. However, the western Sargasso Sea locations simulated by the authors (28°N, 78°W, 40°N, 73°W, 46°N, 45°W), at least one of which appears to have been erroneously reported, are not consistent with the center of distribution of eel leptocephali (Figure 1) [4]. Thus, the conclusion of Naisbett-Jones *et al.* [1], that “the orientation of juvenile eels varies in response to subtle differences in magnetic field intensity and inclination angle along their marine migration route” is unfounded because these are not the fields that the great majority of migrating eel leptocephali would encounter [4]. Further, Naisbett-Jones *et al.* [1] state that the “field corresponding to the Sargasso Sea breeding grounds elicited southwestward orientation” (panel A in their Figure 1). However, this is inconsistent with the distribution pattern of European eel leptocephali, which demonstrates that some of them move northwestward into the Gulf

Stream system while others move directly to the northeast in eastward countercurrents [4].

Naisbett-Jones *et al.* [1] used an ocean circulation model “to place observed orientation responses into an environmental context” and used the swimming direction as a random value in a 120–220° sector centered on the average found in the orientation experiment at location A or B. In any such modelling exercise, the choice of initial conditions is critical [5], and we have several concerns with the choices made by Naisbett-Jones *et al.* [1] Specifically, the dates on which the particles were released (May) do not match the spawning period, which peaks in February–March [6]. Moreover, the study used three non-consecutive HYCOM years, without any justification or rationale for their choice, a number that is too low for probabilistic simulations that would account for the interannual variability of arrival success characteristic of this species [6–8]. For these reasons, the model simulations as conducted by the authors cannot be used to contextualize the observed orientation responses.

Several obvious confounding external factors associated with the experimental set up cannot be ruled out as alternative explanations for the

observations. For example, removal of the central cylinder could have triggered an escape reaction from the eels: eels appear to escape in a direction that is opposite of the hand of the observer (<http://newatlas.com/eels-navigate-magnetism/49014/>). Further, based on the data presented in Naisbett-Jones *et al.* [1] (Figure 1), we calculated that eels had a median orientation of 210° in three of the four magnetic fields that were tested. This is inconsistent with the authors’ conclusion that there was “a significant difference in the orientation of eels in the four magnetic fields” [1]. Rather, it strongly suggests that the eels were orienting according to a confounding topographical cue.

Finally, Naisbett-Jones *et al.* [1] did not analyze their data with respect to the tidal cycle, which is one of the factors that influence the behaviour of glass eels migrating upstream [9]. This is of special concern since the magnetic orientation of glass eels shifts with the tide [10]. Following from all of the above, we conclude that whether European eel leptocephali use the Earth’s magnetic field to guide their migration remains an open question.

AUTHOR CONTRIBUTIONS

Drafting of the manuscript: C.D., H.B.
Critical revision: S.B., C.B., M.C., F.D., W.D., E.D., M.M., C.P., R.H., A.M., A.B.S., H.W., H.W.

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Correspondence Response to Durif *et al.*

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Our recent study [1] in *Current Biology* used a magnetic displacement experiment and simulations in an ocean circulation model to provide evidence that young European eels possess a ‘magnetic map’ that can aid their marine migration. Our results support two major conclusions: first, young eels distinguish among magnetic fields corresponding to locations across their marine range; second, for the fields that elicited significantly non-random orientation, swimming in the experimentally observed direction from the corresponding locations would increase entrainment in the Gulf Stream system. In their critique, Durif *et al.* [2] seem to conflate the separate and potentially independent ‘map step’ and ‘compass step’ of animal navigation. In the map step, an animal derives positional information to select a direction, whereas in the compass step the animal maintains that heading [3,4]. Our experiment was designed such that differences in eel orientation among treatments would indicate an ability to use the magnetic field as a map; the compass cue(s) used by eels was not investigated.

Durif *et al.* [2] contend that the eels’ orientation might have been influenced by topographical or methodological artifacts. Indeed, like all laboratory experiments, ours was conducted in an artificial environment, which can add noise or bias, making it more difficult to elicit and detect statistically significant differences in animal orientation among treatments. Adhering to basic principles, we designed our experiment to hold constant or randomize all conditions likely to affect juvenile eel behavior: time of day (and thus phase of tide), water temperature and chemistry, the direction from which the central holding cylinders were removed, position of arenas, etc. A single factor, the magnetic field, was systematically varied across the experimental treatments. Thus, while any number of factors may have played a role in the orientation displayed by eels, only

the changes to ‘map information’ of the magnetic field (total field intensity and inclination angle) could be responsible for differences in orientation among treatments.

Similar to other magnetic orientation experiments [4–6], variation in orientation was observed among individuals within each magnetic treatment. Despite this variation and any bias, regardless of their sources, we observed statistically significant differences in orientation across the four field treatments ($\chi^2 = 49$, $p = 0.037$) and between two of the six pairwise comparisons (Sargasso Sea vs. NW Atlantic, $\chi^2 = 33$, $p = 0.00052$; NW Atlantic vs. Mid-Atlantic $\chi^2 = 23$, $p = 0.019$).

In what seems to stem from their misunderstanding of a magnetic map [4], Durif *et al.* [2] offer an alternative explanation for our experimental findings: “the contradictory mixture of inappropriate physical and geomagnetic signals confused the late-stage glass eels”. This proposition still requires that eels detect subtle differences in magnetic map information and for those differences to elicit a change in orientation. Thus, Durif *et al.* [2] unwittingly echo our claim that eels possess a magnetic map [1]. Their further criticisms only relate to the interpretation of this central finding.

Our experiment used ‘glass eels’ captured at the end of their marine migration in the Severn estuary, whereas our simulation explored the movement ecology of ‘leptocephali’ larvae at the beginning of their marine migration. Ideally, studies like ours would use the same life stage in the experimental and simulation elements, but given the life histories of most marine migrants, doing so is typically logistically impossible. Uncovering the role of magnetic maps in long-distance marine migrants has relied upon species with terrestrial or freshwater life-stages that are available for experimentation [3]. European eels have not been successfully bred in captivity; finding, collecting and transporting larvae from the open sea would be prohibitively expensive; and keeping larvae alive in the laboratory is notoriously difficult. In contrast, glass eels are readily accessible, easily maintained in captivity, and amenable to behavior experiments.

Citing one of their critique’s co-authors [7], Durif *et al.* [2] suggest it is unrealistic to expect that the sensory systems of larval and glass eels are sufficiently