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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

similar or ontogenetically integrated to warrant studies such as ours. It is possible that larval, juvenile and adult eels possess completely independent and reciprocally uninformative magnetic sensory systems. However, that scenario is incompatible with a hypothesis put forward in the same paper [7] — that leptocephali detect magnetic map information, retain it through ontogeny and use it as a navigational cue during the spawning migration [7]. Alternatively, it is possible that eels, and other marine migrants, possess magnetic sensory systems that, regardless of developmental nuances, retain, transmit and use information across ontological stages. Given existing empirical evidence for eels, the obvious advantage of informational transfer and the fitness consequences of failing to migrate between rearing and spawning habitats, we suspect that the latter scenario is more likely.

There are precedents for individuals of one life stage responding with oriented movement to magnetic fields they encounter during a different life stage [3–6]. Hatchling sea turtles [5] and stream-stage juvenile salmon [6] that have never been in the ocean respond to magnetic displacements with orientation that is suitable to aid foraging and migration during the marine phases of their life-histories, despite those magnetic fields not being encountered naturally until their marine migrations months or years later. Indeed, animals respond adaptively to magnetic fields that exist across their marine range before the onset of migration [5,6], after its completion [1] and in life-stages not undertaking long-distance movements [1,6]. Understanding how these systems operate through ontogeny (e.g., mature individuals might need to orient differently than juveniles to certain magnetic fields), how they are inherited, and how they evolve are outstanding research challenges that will be met using a variety of taxa and approaches [3].

The locations for magnetic displacements were chosen to test the possibility that magnetic map information could be used by eels to influence their chances of entering the Gulf Stream. Regrettably, there was a typographical error for the longitude of the Sargasso Sea magnetic field that may have introduced confusion (this location was correctly shown in our figures and in

Supplemental table S1 as N 28°, W 70° — rather than W 78° in the Experimental procedures). Nonetheless, the locations of test fields are near the periphery of the marine range where oriented swimming may be most critical for survival [5,6]. Durif *et al.* [2] argue that the direction of swimming elicited by the Sargasso Sea magnetic field is incompatible with the observed larval distribution, presumably because they believe southwestward swimming near the southern boundary of their oceanic habitat necessarily causes eels to move beyond their known range. However, the movement of marine organisms is the product of swimming and ocean velocities [5]. The combination of the eel's weak swimming and more powerful ocean currents likely results in eels moving northward (and eventually eastward) with the Gulf Stream System, rather than steadily southward.

To demonstrate observed orientation increases entrainment of eels in the Gulf Stream, we simulated swimming at a conservative speed and across a range of oceanographic conditions that eels likely encounter. Durif *et al.* [2] suggest that we should have used earlier start dates for our simulations, but their concern on this point is puzzling. Whether adult eels spawn in February–March or later in the year is immaterial. The dates we chose (May) accurately reflect when larval eels are in both the Sargasso Sea and the NW Atlantic at the sizes relevant to the swimming speeds simulated [8,9]. Durif *et al.* [2] go on to state that we should have used more than three years in our simulations. However, the number of years that should be used for dispersal simulations depends on the question being asked. We chose three non-consecutive years to reduce temporal autocorrelation across simulations and sample a range of oceanographic conditions. This was sufficient to detect a large effect of oriented swimming on entry into the Gulf Stream; a more subtle effect might have required simulations of additional years. Following established methods and using a combination of years and depths appropriate for testing our stated question of interest, we found that in each of the 18 paired passive-swimming simulations (three depths x three years x two regions), swimming increased entrainment into the Gulf Stream. The likelihood that such an

outcome would occur by chance is vanishingly low (Sign Test, $p = 0.00002$).

Our magnetic displacement experiment provides the first evidence that eels derive positional information from Earth's magnetic field, and thus have a 'magnetic map' [3,4]. Our simulations showed using this map to orient swimming can increase entrainment in the Gulf Stream. The experiment and simulations were appropriate and informative, and we stand by our results and conclusions.

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