BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2020), **95**, pp. 1273–1286. 1273
doi: 10.1111/brv.12609

A comprehensive hypothesis on the migration of European glass eels (*Anguilla anguilla*)

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ABSTRACT

The European eel (*Anguilla anguilla*) is a catadromous fish that spawns in the Sargasso Sea. As larvae, eels cross the Atlantic Ocean and reach the continental slope of Europe, where they metamorphose into post-larval glass eels. These reach the continent, where some enter fresh water, some remain in marine waters, and others move between fresh and marine waters. After 5–25 years, as adult silver eels, they migrate back from fresh water to the Sargasso Sea to spawn and die. The glass eel stage is a critical step during which the eels cross the continental shelf and recruit to estuaries, where they facultatively transition to fresh water. Extensive research has been conducted to understand the behavioural mechanisms and environmental cues that aid and guide glass eels' migration. Glass eels follow odours and salinity gradients, they avoid light, and they change orientation and depth according to the tides. Recent work revealed that European glass eels also use Earth's magnetic field and lunar cues to orient. However, while we understand many aspects of their orientation behaviour, a unifying theory describing how glass eels migrate from the continental slope to fresh water is lacking. The goal of this review is to develop a comprehensive hypothesis on the migration of European glass eels, integrating previous knowledge on their orientation behaviour with recent findings on magnetic and celestial orientation. This review follows the journey of a hypothetical glass eel, describing the nature and the role of orientation cues involved at each step. I propose that, although glass eels have the sensory capacity to use multiple cues at any given time, their migration is based on a hierarchical succession of orientation mechanisms dictated by the physical properties of the environments that they occupy: (*i*) lunar and magnetic cues in pelagic water; (*ii*) chemical and magnetic cues in coastal areas; and (*iii*) odours, salinity, water current and magnetic cues in estuaries.

Key words: European eel, migration, fish behaviour, glass eel, orientation, catadromous

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I. INTRODUCTION

The European eel (*Anguilla anguilla*) is a catadromous fish that undertakes one of the most extraordinary migrations in the animal kingdom, and constitutes a major fishery in Europe (Starkie, 2003). This species has been subject to fishing and farming practices for millennia (Dekker, 2003, 2018). However, the European eel is now critically endangered [International Union for Conservation of Nature (IUCN)] and its population has decreased dramatically since the 1980s (Drouineau *et al.*, 2018; ICES, 2018). The reasons of this decline are still unclear, but it has been suggested that habitat modification, migration barriers, and fisheries might play a role (Starkie, 2003). The EU established a recovery plan in 2007, and monitoring programs as well as models of stock dynamics have been created to assess the effectiveness of the European protection framework (Dekker, 2018). To this end, knowledge of the migratory strategies that early life stages adopt is essential to understand, and possibly predict, the recruitment of the European eel to fresh water.

This species has been shrouded in mystery for millennia, stimulating curiosity and interest since at least the 4th century BC. At that time, the Greek philosopher Aristotle hypothesized in his *History of Animals* that eels originate through spontaneous generation from non-living matter, specifically, from mud. This hypothesis was linked to the fact that the eel has an extremely complex life cycle (Fig. 1) such that, in ancient Greece, philosophers and men of science were not able to link the eels to their early life stages. Two thousand years later (1886–1896) Yves Delage and Giovanni Grassi determined, for the first time, that the leaf-shaped creature called *Leptocephalus brevirostris* was actually the larval form of *Anguilla anguilla* (Bertin, 1965).

The struggle that scientists encountered in understanding the biology of the European eel was rooted in the multiple physiological and habitat changes that this species undergoes and that it nearly crosses the entire Atlantic Ocean twice, first as a larva and finally as an adult. The European eel shares the same life history with several temperate species/subspecies of catadromous eels of the genus *Anguilla*, which are widely distributed around the world (Tesch, 1977; Watanabe, 2003). Because of their similarity and phylogenetic relatedness, closely related eel species are referred to herein when analogous studies on the European eel are not available.

The European eel spawns in the Sargasso Sea, and then migrates more than 5000 km towards the European coast (Schmidt, 1923; Miller *et al.*, 2015). The breeding area of this species partially overlaps with that of the closely related American eel (*Anguilla rostrata*) (Miller *et al.*, 2015), whose juveniles enter North American streams (Tesch, 1977). After hatching in the Sargasso Sea, European eel leptocephali drift with the Gulf Stream (Tesch, 1977; Bonhommeau *et al.*, 2010) until they reach the continental slope of Europe and North Africa. There, the larvae metamorphose into the post-larval transparent glass eel (Tesch, 1980). Glass eels then start a complex journey, migrating from the continental slope, crossing the continental shelf, and eventually reaching coastal areas (Deelder, 1952; Tesch, 1977). After reaching the coast, glass eels recruit in estuarine environments, where some of them will start their upstream migration into fresh water (Tzeng *et al.*, 2000). Here, in brackish water, they pigment into juveniles, known as elvers (Tesch, 1977). The body of the eel becomes wider, it develops skin pigment and the jaw enlarges, the composition of visual pigments changes, and they adapt their physiology to fresh water (Wood, Partridge, & Grip, 1992; Ciccotti *et al.*, 1993). Thus, the eel develops all of the morphological and physiological features necessary for life in fresh water. However, some eels display facultative catadromous behaviour, remaining in marine waters throughout their life, while some switch between fresh and salt water (Tsukamoto & Arai, 2001; Daverat *et al.*, 2006; Thibault *et al.*, 2007; Marohn, Jakob, & Hanel, 2013).

The eels that enter fresh water will spend most of their lifetime there (5–25 years or more), to grow into the adult stage of the yellow eel first, then metamorphose into silver eels (Tesch, 1977; Durif *et al.*, 2009), and then start developing towards sexual maturity during the migrating silver eel stage. Females, which are larger, reach maturity at an older age (on average) than smaller males (Vøllestad, 1992; Arai, Kotake, & McCarthy, 2006). Age at maturity also varies with growth rate and, therefore, increases with latitude (Vøllestad, 1992). Silver eels exhibit all of the morphological features of a mesopelagic, mid/deepwater fish. The eyes increase in size, and the number of photoreceptors as well as the diameter of rods increases making them more efficient in low-light conditions (Pankhurst, 1982). Moreover, the body develops the countershading typical of pelagic fish. The silver eel is the adult migratory stage, which swims across the Atlantic ocean to the spawning area in the Sargasso Sea (Schmidt, 1923; Righton *et al.*, 2016; Béguer-Pon *et al.*, 2018), where they die after spawning (Fig. 1).

Deeper knowledge of the behaviour of the European eel is required for a better understanding of its migratory strategies. Great advances were made in the 20th century in our knowledge of the behaviour and movement ecology of this species. Extensive sampling programs were conducted in the Atlantic Ocean to understand the horizontal and vertical movement of eel leptocephali (Hanel *et al.*, 2014; Miller *et al.*, 2015), and direct observations of the migratory behaviour of yellow and silver eels were made through the use of telemetry (Amilhat *et al.*, 2016; Righton *et al.*, 2016; Béguer-Pon *et al.*, 2018). However, less is known about the migratory behaviour of glass eels during their complex journey from the continental slope to estuaries.

Several laboratory studies have described the cues used by glass eels with special focus on chemical cues, such as odours (e.g. green odours, amino acids and bile salts) and salinity gradients (Tosi *et al.*, 1988; Crnjar *et al.*, 1992; Sola & Tosi, 1993; Sola, 1995). Numerous observations from the field come from sampling in brackish and/or fresh water which, together with studies on otolith microstructure, provide valuable insights on such aspects as timing of arrival at the coast, duration of the migration, and timing of metamorphosis. Recent work investigated the orientation abilities of

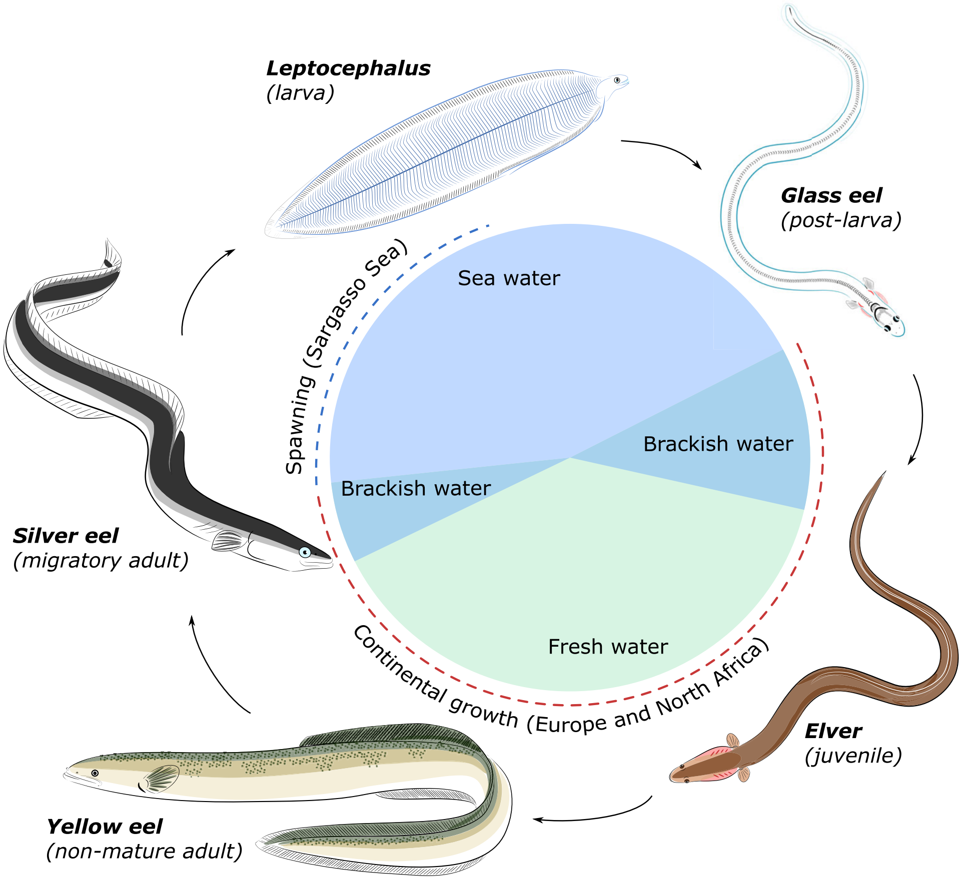


Fig. 1. Life history of the European eel (*Anguilla anguilla*). Eels hatch as leptocephalus larvae in the Sargasso Sea. As larvae, they drift across the Atlantic Ocean to the continental slope of Europe, where they metamorphose into post-larval, transparent glass eels. The glass eels migrate across the continental shelf and eventually reach the brackish water of estuaries. After metamorphosing into pigmented juveniles (elvers), they start the ascent into fresh water, where they grow into adult yellow eels. After some years, yellow eels undergo another metamorphosis into silver eels, which migrate for thousands of kilometers to the Sargasso Sea where they spawn and die.

glass eels with respect to the Earth's magnetic field (Cresci *et al*., 2017, 2019*a*) and lunar cues (Cresci *et al*., 2019*b*), at sea and under laboratory conditions, suggesting that glass eels may use both magnetic and lunar orientation mechanisms during migration.

However, while many single pieces of the complex puzzle that underlies the orientation and migratory behaviour of glass eels have been elucidated, a holistic hypothesis describing how European glass eels migrate from the continental slope to estuaries is lacking. In this review, I integrate the existing body of literature on the behaviour of glass eels with recent findings on magnetic and lunar-driven orientation and propose a comprehensive theory. I hypothesize that the migration of glass eels is a multistep, hierarchical succession of orientation mechanisms involving multiple external cues operating at different spatiotemporal scales. I propose that, although glass eels have the sensory ability to use multiple environmental cues, they use different subsets of those cues and orientation mechanisms at any given time, according to the physical properties of the environment at each specific step of the migration, from the continental slope to estuaries. This will be presented by following the journey of a hypothetical glass eel in space and time during its migration. Thus, I first review aspects about the metamorphosis from leptocephali into glass eels that are relevant to understanding how the journey of glass eels begins. Next, I suggest how glass eels might use lunar signals, odours, salinity gradients, water currents and Earth's magnetic field (EMF) to navigate from pelagic shelf waters to shallow estuaries. Finally, I describe the orientation dynamics associated with residency in estuaries, where glass eels become pigmented into elvers.

II. METAMORPHOSIS FROM LEPTOCEPHALUS TO GLASS EEL ON ARRIVAL AT THE CONTINENTAL SLOPE

In the Sargasso Sea, the smallest eel leptocephali are distributed in the water column at depths ranging between 50 and

300 m and do not display diel vertical movement when smaller than 5 mm (Castonguay & McCleave, 1987). At lengths between 5 and 20 mm, leptocephali are found at 100–150 m during the day and 50–100 m during the night (Castonguay & McCleave, 1987). The vertical migratory behaviour in the Sargasso Sea does not vary significantly between leptocephali of the European eel and those of the American eel (Castonguay & McCleave, 1987), which have partially overlapping spawning areas. The horizontal swimming behaviour of the leptocephali of these two closely related species remains unknown, and whether a differing orientation behaviour between the two plays a role in determining the direction of their migrations towards Europe and North America, respectively, remains a mystery. European eel leptocephali larvae cross the Atlantic Ocean from the spawning areas in the Sargasso Sea to the European continental slope, where they undertake a metamorphosis into glass eels (Fig. 2A, Step 1). Researchers started studying this metamorphosis over a century ago (Schmidt, 1906), and several aspects such as the timing of the metamorphosis, the age and the spatial distribution (vertical and horizontal) of metamorphosing larvae, were partially described. However, the environmental conditions that trigger this event, and the behaviour and orientation strategies the metamorphosing larvae use to move towards the coast remain unknown. Otolith microstructure and microchemistry analyses indicate that the metamorphosis of leptocephali larvae into glass eels may take 18–52 days (Arai, Otake, & Tsukamoto, 2000). However, estimates of timing based on otolith microstructure might require further validation as otolith size increments vary with water temperature (Fukuda *et al*., 2009) and age estimates based on these techniques appear to be inconsistent with estimates from at-sea sampling studies (McCleave, 2008). During this period, they swim at greater depths during the day and shallower depths during the night (Castonguay & McCleave, 1987). When they reach the proximity of the European continental slope, they descend to depths of 300–600 m during the day and ascend to 35–100 m during the night (Tesch, 1980). This diel vertical migration appears to be conserved throughout metamorphosis, as glass eels show similar patterns of vertical distribution in coastal water, influenced by both light and tides (Creutzberg, 1961; Bardonnet, Bolliet, & Belon, 2005).

Sampling cruises conducted with midwater trawls provided important information on the areas where metamorphosis occurs. Between 1971 and 1977, data from cruises off the Iberian coast using an Isaacs–Kidd Midwater Trawl indicated that metamorphosis occurs offshore of the continental slope (Tesch, 1980). Specifically, leptocephali were collected outside the margins of the shelf but only one glass eel was found over the shelf (Tesch, 1980). Sampling conducted in 1991 with the same trawls off the Iberian coast, performed at depths of 50, 75 and 100 m, confirmed that leptocephali can be found offshore of the slope (more abundant at 100 m) (Antunes & Tesch, 1997*b*). However, while leptocephali undertaking metamorphosis almost never occur over the continental shelf (Antunes & Tesch, 1997*a*; Miller *et al*., 2015), glass eels can be found beyond the continental shelf margin in pelagic waters, from 50 to more than 1000 m deep and up to 300–600 km offshore of the slope (Antunes & Tesch, 1997a, 1997b). Thus, while the end point of the distribution area of metamorphosing leptocephali has been identified as the continental shelf, the areas and the environmental triggers associated with the beginning of the metamorphosis from leptocephalus to glass eel are not well known.

During metamorphosis, as the buoyancy of glass eels and the kinetics of their swimming (anguilliform swimming) differ from those of the larvae, changes in swimming strategy and behaviour might also occur. As leptocephalus larvae, eels are adapted to live in the upper layers of the mesopelagic zone (down to 600 m). Experiments on early life stages of Japanese eel (*A. japonica*), a closely related species with the same morphological features as *A. anguilla*, revealed that from the earliest larval stages, leptocephali continuously increase in buoyancy as their body length increases, becoming positively buoyant at approximately 30 mm in total length (Tsukamoto *et al*., 2009). However, as metamorphosis begins, buoyancy starts to decrease, crossing a phase of neutral buoyancy finally to become negatively buoyant as glass eels (Tsukamoto *et al*., 2009). When larvae undertake metamorphosis into glass eels, the body structure changes dramatically: the body surface shrinks, cartilage turns into bone, and the cross section of the body becomes cylindrical (Tesch, 1977). All of these changes increase the density of the body. Glass eels remain negatively buoyant and do not develop a fully functional (gas-filled) swim bladder until they reach fresh water (Hickman, 1981). All of these modifications suggest that the buoyancy control of glass eels relies only on their swimming abilities, which at this stage play a key role in their movement ecology.

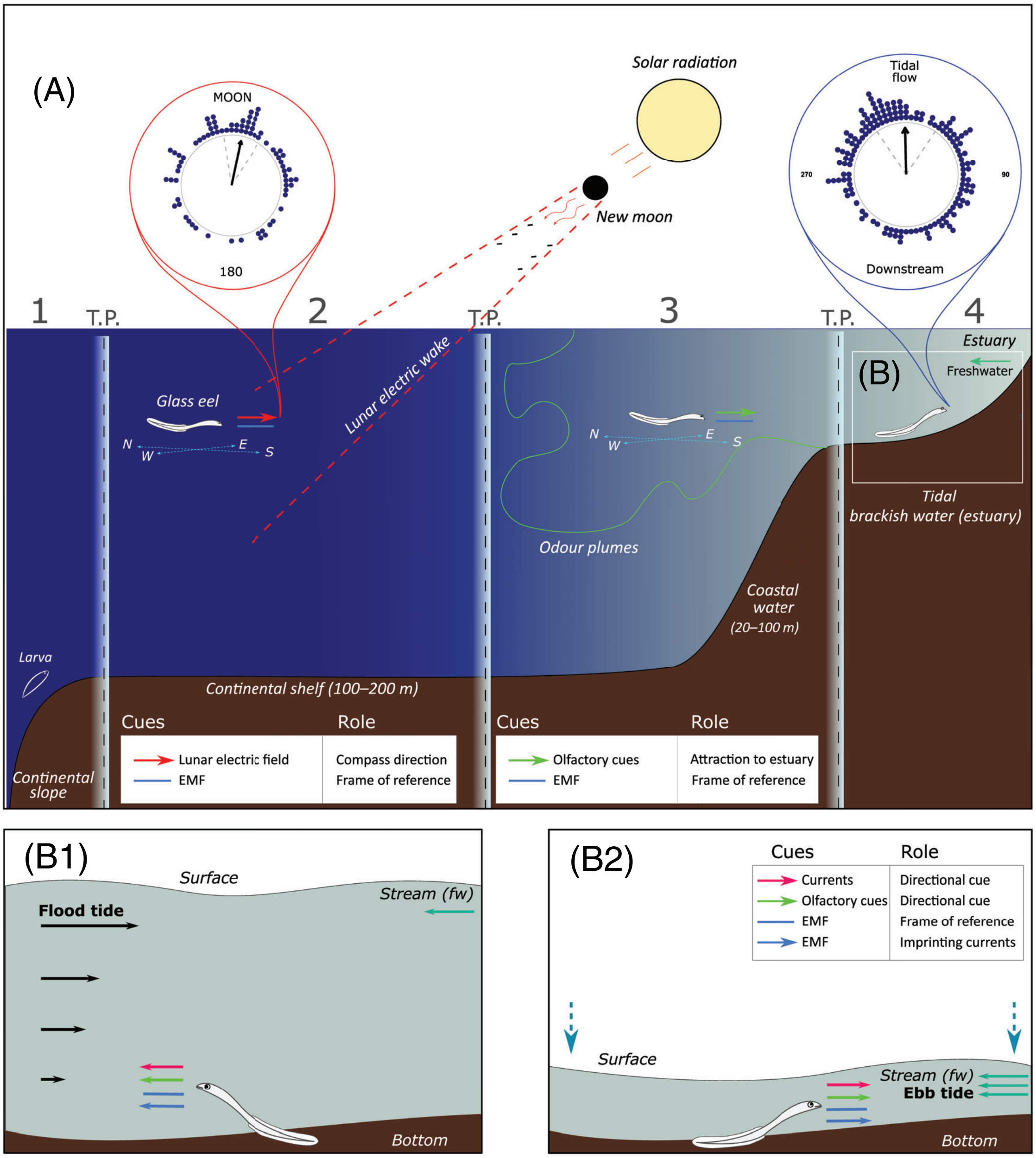
At metamorphosis, the behaviour of this fish switches from a larval phase, which feeds and mainly drifts with ocean currents, to a non-feeding, actively migrating stage, which crosses the shelf and recruits to the coast (Tesch, 1977; Miller, 2009). This event represents the beginning of the journey of glass eels, which navigate through a great variety of environments relying on complex, multisensory orientation mechanisms.

III. OVER THE CONTINENTAL SHELF: LUNAR AND MAGNETIC CUES IN PELAGIC WATER

Once metamorphosis has occurred, glass eels cross the continental shelf, moving from the continental slope towards coastal water. This is the least understood phase of the migration as most glass eel sampling has been conducted at stations located in estuaries or further into fresh water, where they become pigmented (Harrison *et al*., 2014). However, there is some information on the vertical distribution of glass eels swimming in open water, especially around the continental slope. Glass eels can be found at depths ranging between

50 and 1000 m when offshore of the shelf (Antunes & Tesch, 1997a, 1997b). More in proximity to the slope, one glass eel was collected SW of the Isle of Ouessant in 1974 at a depth of 140 m (Tesch, 1980). While moving over the shelf, glass eels ascend the water column and swim at shallower depths. Glass eels were sampled at the entrance of the Baltic Sea, in the Skagerrak and Kattegat areas, at depths down to 50 m (Hagstrom & Wickström, 1990). More inshore, in the shallow coastal area of the Dutch Wadden Sea, glass eels were found from the surface down to 8 m, displaying patterns of vertical movement which followed tidal and light cycles (Creutzberg, 1961).

However, while there is some indication of how glass eels move vertically at sea, there is almost no information on whether they perform horizontal orientation during this pelagic phase. This is because glass eels are too small and fragile for today's tagging-telemetry technology, and observing their behaviour at sea remains challenging. The only data on horizontal orientation of glass eels at sea available to date come from studies conducted in the Norwegian area of the North Sea (Cresci *et al.*, 2017, 2019*b*). These studies indicate that glass eels use orientation mechanisms based on Earth's magnetic field and possibly the lunar cycle, which are both



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cues that are available in open water. Specifically, glass eels have an internal magnetic compass that they use for orientation and which changes direction according to the tidal phase, with a southerly heading during the ebb tide (Cresci *et al.*, 2017). This means that glass eels can sense the direction of the earth's magnetic north, east, south and west.

Behavioural tests on the orientation of glass eels at sea conducted throughout the lunar cycle indicate that their orientation direction is linked to the lunar phase (Cresci *et al.*, 2019*b*). This adds to a large body of literature reporting a connection between moon phases and activity patterns of the eel at all life stages. The lunar cycle affects leptocephalus larvae, which hatch in the open ocean and change their depth according to the phase of the moon, swimming deeper during full-moon nights (Kracht, 1982; Tsukamoto *et al.*, 2003). The arrival of glass eels at the coast is lunar dependent, with peaks of abundance at new and full moons (De Casamajor, Bru, & Prouzet, 2001; Yamamoto, Mochioka, & Nakazono, 2001; Jellyman & Lambert, 2003), and at the stage of yellow and silver eels (adult stage) the migratory behaviour of the eels changes according to the moon phase, both at sea and in fresh water (Tesch, 1989; Bruijs & Durif, 2009; Verhelst *et al.*, 2018). In fresh water, silver eels migrate downstream mostly with the ebb tide during both the full and new moon (Verhelst *et al.*, 2018). During their marine migration, silver eels swim slower and closer to the bottom (at depths that can be >400 m) during the full moon (Tesch, 1989).

Observations of glass eels *in situ* revealed that they orient towards the moon azimuth and in an average southward direction at the new moon, when the moon is invisible and above the line of the horizon (Cresci *et al.*, 2019*b*). The moon azimuth could provide glass eels with a magnetic direction towards which they swim under these phases of the lunar cycle when the moon is above the horizon (Cresci *et al.*, 2019*b*) (Fig. 2A, Step 2). Glass eels might also remember this direction using the magnetic compass as their frame of reference when the lunar phase switches and the moon is no longer detectable. As the lunar-related orientation was observed at the new moon, these findings indicate that the mechanism is not based on vision, rather it could depend on global-scale disturbances in electrical fields (Cresci *et al.*, 2019*b*). However, this hypothesis needs to be tested by observing the orientation of glass eels in the laboratory under an artificial electric field with the same characteristics as those caused by the motion of the moon.

The path of the moon above the horizon, at new moon, in the Northern hemisphere begins in the east (moonrise), continues southward, and ends west (moonset). Therefore, following the moon under these specific conditions results in glass eels orienting (on average) towards the south. The advantages of this orientation mechanism are still unknown, but considering the large and mesoscale ocean circulation around Europe, from the North Atlantic drift (which flows northeastward) to the end of the Azores Current (which flows

(Figure legend continued from previous page.)

Fig. 2. Diagram of the orientation behaviour and mechanisms of glass eels (*Anguilla anguilla*) at different steps of their migration. This schematic figure shows all of the steps in the migration of glass eels from the continental slope up to estuaries. The diagram is theoretical and does not apply to a specific geographical area. This figure does not take into account vertical movement related to selective tidal stream transport (STST), as it focuses on horizontal orientation. (A) Numbers indicate the steps of the migration, which are separated by vertical dashed lines. T.P., transition phase between steps. The colour-coded cues involved at each step are designated by arrows (if the cue serves as a directional cue) and lines (if the cue acts as frame of reference). Dashed blue arrows with the cardinal points (N, E, S, W) represent glass eels' magnetic compass, an orientation mechanism that glass eels possess at all steps. Step 1: leptocephali reach the continental slope and metamorphose into post-larval glass eels. Step 2: glass eels swim across the continental shelf in pelagic water. Glass eels orient towards the azimuth of the moon at the new moon. The plot of the orientation response of glass eels *in situ* with respect to the moon azimuth described in Cresci *et al.* (2019*b*) is also shown (red circle), with the blue data points showing the angle between the orientation of the glass eels and the azimuth of the moon (0°, top of the plot), the black arrow showing the average direction of the glass eels and the grey dashed lines the 95% confidence intervals. At this step, the moon azimuth might serve as a directional cue (red arrow) coupled with the magnetic compass (Earth's Magnetic Field, EMF), which could act as a frame of reference (blue line). Lunar-related orientation was hypothesized to depend on the moon's electric wake (red dashed lines). Step 3: closer to the coast, glass eels might predominantly follow odour plumes and salinity gradients (olfactory cues, green arrow). Step 4: when glass eels reach the estuaries (B), they use multiple orientation cues. Here, the alternation of flood and ebb tides causes changes in water depth, switch of current direction and alternation of different combinations of odours and salinity gradients. Rheotaxis (orientation to water current, fuchsia arrow) is one of the main components of the orientation of the eels at this step. During flood tide (B1), the water gets deeper and saline currents flow from the seaward side of the estuary into the estuary (black arrows). However, the current from the stream with fresher water (fw, light green arrow) still flows in the opposite direction, potentially closer to the surface. If glass eels perform station-holding behaviour, they orient against the prevailing current (flooding current). They accomplish this using rheotaxis, detecting odours and/or salinity gradients transported by the flooding current, and imprinting the magnetic direction of the flow using the magnetic compass as a frame of reference. This behaviour at the estuary is also exhibited when the tide switches to ebb tide (B2), during which the water becomes shallower and the current faster and dominated by fresher water from the stream. The plot of the orientation response associated with learning the magnetic direction of tidal flows (magnetic imprinting) that occurs at this step is shown in the blue circle (Step 4, B) (from Cresci *et al.*, 2019*a*). The plot shows the magnetic orientation of glass eels with respect to the direction of the flow (magnetic upstream = 0°, magnetic downstream = 180°). Glass eels form a memory of the magnetic direction from which the tidal currents flow and swim towards that direction (magnetic upstream).

east-northeastward), orientation towards the south could help glass eels recruit to coastal areas independent of latitude. This hypothesis will be tested in the future using bio-physical dispersal models.

IV. NAVIGATING COASTAL WATER: ODOURS AND SALINITY GRADIENTS

Eels possess one of the most sensitive olfactory systems among fishes, and olfaction plays a central role in their life (Huertas, Canário, & Hubbard, 2008). At the larval (leptocephalus) stage eels already possess 12–15 folds in the olfactory epithelium (Tesch, 1977), which is the same number possessed by adult salmonids, well known for their acute olfaction (Dittman & Quinn, 1996; Ueda, 2012). Additionally, comparing olfaction in relation to vision in adults, the ratio of the surface area of the olfactory epithelium (OE) compared to the surface area of the retina in the eye ranges between 14 and 140 in freshwater fish, but in eels this ratio is more than 600 (Tesch, 1977). At the glass eel stage, the OE is also well developed, with both ciliary and microvillar receptors at the centre of the olfactory lamellae, and cell aggregates that are likely to be precursors of ciliated supporting cells and receptors in the periphery (Sola, Giulianini, & Ferrero, 1993). Eels can detect highly diluted olfactory cues and exhibit different thresholds for detection depending on the chemical (Table 1). Their sensitivity to olfactory cues varies throughout the life cycle depending on sex, life stage, environment (fresh water, sea water) and maturation.

After crossing the pelagic area over the continental shelf, glass eels reach shallower, coastal water during the spring, where they encounter water masses with a broad range of characteristics. The European coast along which glass eels recruit is very diverse in terms of bottom topography, physical/chemical and biological features (Babin *et al.*, 2003). Furthermore, freshwater discharge also varies greatly along the European coast, depending on location. As an example, basins like the Baltic Sea and areas surrounding main European rivers are influenced by large freshwater discharges (Hordoir *et al.*, 2013). These rivers transport odours and create salinity gradients, which can serve as orientation cues for both adult fish (Dittman & Quinn, 1996) and late-stage fish larvae (Paris *et al.*, 2013; Foretich *et al.*, 2017). Unlike anadromous fishes, catadromous eels do not migrate to a freshwater site of previous occupancy (homing) or that is tied to a specific genetic lineage. European eels belong to the same panmictic population and, as glass eels, distribute over a broad latitudinal range. Therefore, it is likely that eels are attracted to freshwater habitats by a general set of environmental cues rather than one predominant cue attracting glass eels to freshwater habitats.

As a glass eel, *A. anguilla* could rely on odours to navigate coastal waters up to estuaries (Fig. 2A, Step 3), and extensive research has been conducted to investigate the behaviour of glass eels of multiple species in relation to odours (Table 1). Glass eels of the European eel respond to a broad variety of chemical cues, such as salinity gradients (Sola & Tongiorgi, 1996). The attraction of glass eels to fresh water varies among individuals and is associated with higher locomotory activity and reduced growth rate (Edeline, Dufour, & Elie, 2005b). Moreover, glass eels coming from the sea and adapted to salt water seem to be less attracted to fresh water compared to individuals that are already adapted to fresh water (Tosi *et al.*, 1988).

Glass eels are also attracted to inland odours, which could be associated with the flora and micro fauna responsible for decomposition of detritus in fresh water (Sorensen, 1986). The attraction to odours is dependent on the salinity of the water. Inland odours such as geosmin (trans-1,10-dimethyl-trans-9-decalol) attract glass eels (Tosi & Sola, 1993; Sola, 1995), and could play a role in migration to estuaries. Geosmin is a green odour, which are volatile substances with distinct green, earthy or musty odours, produced by actinomycetes, algae or bacteria (Sola, 1995). Interestingly, geosmin seems to be an attractant in fresh water but a repellent in sea water (Tosi & Sola, 1993). However, maze-choice experiments on the closely related New Zealand species *A. australis* (shortfin eel) and *A. dieffenbachii* (longfin eel) show that neither of these two species responded to geosmin, indicating that attraction to inland odours might depend on habitat and species (McCleave & Jellyman, 2002).

One of the main hypotheses for the migration of catadromous and anadromous fish into fresh water is the 'pheromone hypothesis', which proposes that fishes from different life stages release particular odours into the water (pheromones) that function as attractants for conspecifics which are migrating towards fresh water. The pheromone hypothesis has been associated with the homing migration of anadromous salmonids for almost a century (White, 1934). Population-specific pheromones released by downstream-moving salmon smolts purportedly function as olfactory cues for adults on their spawning migration, helping them find their natal stream (White, 1934; Nordeng, 1977; Stabell, 1984; Quinn, 1990). However, this pheromone-based homing mechanism for salmon remains controversial (Quinn, Brannon, & Whitman, 1983; Stabell, 1984; Brannon & Quinn, 1990; Quinn, 1990). The pheromone hypothesis is also applicable to species that do not return to their natal stream but need to find any freshwater habitat that is suitable for survival and reproduction, despite not having experienced it before. An example of this is the sea lamprey (*Petromyzon marinus*), which does not migrate to natal streams but moves upstream in fresh water guided by olfactory cues (Vrieze, Bjerselius, & Sorensen, 2010). This upstream migration of lampreys is possibly guided by pheromones released by lamprey larvae present in those streams (Bjerselius *et al.*, 2000; Sorensen & Vrieze, 2003). Glass eels also need a more general orientation mechanism compared to anadromous salmon. Glass eels migrate to estuaries that they have never encountered before, where they metamorphose into juvenile elvers and start their upstream migration. Thus, pheromones released by conspecifics living in fresh water

Table 1 List of chemical compounds that cause attraction/repulsion in glass eels. The compound, the odour category to which it belongs, and its role in eliciting behaviour in glass eels are shown. The salinity (FW, fresh water; SW, salt water) at which a specific compound elicits a specific behaviour, and the minimum concentration thresholds at which attraction or repulsion was observed are also indicated

Chemical cue	Odour category	Role	Water	Detection threshold	Reference
Geosmin (trans-1,10-dimethyl-trans-9-decalol)	Earthy odour	Attractant	FW	10^{-13} mg/l	Tosi & Sola (1993)
		Repellent	SW	10^{-13} mg/l	
MMP (2-methyl-3-methoxypyrazine)	Green odour	Attractant	FW	10^{-13} mg/l	Sola (1995); Sola & Tongiorgi (1996)
		Repellent	SW	10^{-13} mg/l	
		Attractant	Brackish (30‰)	10^{-13} mg/l	
		Attractant	Brackish (15‰)	10^{-9} mg/l	
ETMCE (2-isobuthyl-3-1-ethyl-2,2,6-trimethylcyclohexanol)	Green odour	Attractant	FW	10^{-13} mg/l	
		Repellent	SW	10^{-13} mg/l	
		Attractant	Brackish (30‰)	10^{-13} mg/l	
		Attractant	Brackish (10‰)	10^{-9} mg/l	
MT (4-methylthiazole)	Green odour	Attractant	FW	10^{-12} mg/l	
		Repellent	SW	10^{-11} mg/l	
L-MF (L-2-methylfenchol)	Earthy odour	Attractant	FW	10^{-12} mg/l	
		Repellent	SW	10^{-12} mg/l	
D-MF (D-2-methylfenchol)	Earthy odour	Attractant	FW	10^{-9} mg/l	
IBMP (2-isobutyl-3-methoxypyrazine)	Green odour	Attractant	FW	10^{-11} mg/l	
		Repellent	SW	10^{-9} mg/l	
TMCE (1,2,2,6-tetramethycyclohexanol)	Earthy odour	Attractant	FW	10^{-11} mg/l	
		Repellent	SW	10^{-11} mg/l	
IPMCET (4-isopropyl-7-methycyclohexathiazole)	Green odour	Attractant	FW	10^{-10} mg/l	
Fresh water (0‰)	Salinity difference	Attractant	Eels kept in FW		Tosi *et al.* (1988)
D-glutamine	aa (CS)	Attractant	FW	10^{-7} M	Sola & Tongiorgi (1998)
		Attractant	SW	10^{-7} M	
D-glutamic acid	aa (CS)	Attractant	FW	10^{-7} M	
		Attractant	SW	10^{-8} M	
D-asparagine	aa (CS)	Attractant	FW	10^{-7} M	
		Repellent	SW	10^{-7} M	
D-alanine**	aa (CS)	Attractant	FW	10^{-9} M	
		Repellent	FW	10^{-7} M	
		Repellent	SW	10^{-8} M	
β-alanine	aa (CS)	Attractant	FW	10^{-9} M	
		Attractant	SW	10^{-9} M	
L-asparagine	aa (CS)	Stimulant OE	–	10^{-9} M	Crnjar *et al.* (1992)
L-glutamine	aa (CS)	Stimulant OE	–	10^{-9} M	
Conspecific odour (*A. rostrata*)	Conspecific wash	Attractant	FW	0.2 g of glass eels l^{-1} h^{-1}	Schmucker *et al.* (2016)
	Conspecific wash	Attractant	Brackish	6.3 g of elvers l^{-1} h^{-1}	Galbraith *et al.* (2017)
Glycocholate	Bile salts (CS)	Attractant	FW	10^{-11} M	Sola & Tosi (1993)
		Attractant	SW	10^{-10} M	
Taurodeoxycholate	Bile salts (CS)	Attractant	FW	10^{-11} M	
		Attractant	SW	10^{-10} M	
Taurocholate	Bile salts (CS)	Attractant**	FW	10^{-11} M	
Cholate	Bile salts (CS)	Attractant**	FW	10^{-11} M	
		Attractant**	SW	10^{-11} M	
Deoxycholate	Bile salts (CS)	Attractant**	FW	10^{-14} M	
		Attractant**	SW	10^{-10} M	
Glycochenodeoxycholate	Bile salts (CS)	Attractant**	FW	10^{-12} M	
		Attractant**	SW	10^{-11} M	
Taurochenodeoxycholate	Bile salts (CS)	Attractant**	FW	10^{-14} M	

(Continues)

Table 1. *(Cont.)*

Chemical cue	Odour category	Role	Water	Detection threshold	Reference
Taurine	Taurine (CS)	Attractant** Attractant Attractant**	SW FW SW	10^{-12} M 10^{-12} M 10^{-9} M	

aa, amino acid; CS, conspecifics; OE, olfactory epithelium.
*Role changes at different concentrations.

could attract migrating glass eels towards the recruitment estuaries. Glass eels are indeed attracted to odours coming from conspecifics. Two maze-choice experiments showed that glass eels of *A. rostrata* preferred water from 'washes' of conspecifics (Schmucker *et al.*, 2016). Moreover, glass eels are more attracted to more concentrated odours from conspecifics, showing a logarithmic increase in response depending on the concentration of the stimulus (Schmucker *et al.*, 2016). Interestingly, the attraction to conspecifics is stage-dependent as it disappears in pigmented elvers (Schmucker *et al.*, 2016). This was confirmed by another study conducted on glass eels and elvers using a two-choice-maze assay, which demonstrated that glass eels are attracted to odours from both other glass eels and older elvers (Galbraith *et al.*, 2017). However, elvers do not show attraction for other elvers or glass eels (Galbraith *et al.*, 2017). These results suggest that glass eels could use odours from conspecifics for their migration in coastal areas, but that when they pigment into elvers this behaviour changes and new cues possibly become dominant.

In the context of the pheromone hypothesis, amino acids are potential candidate compounds that might act as pheromones. Electro-olfactogram records from glass eels show that L-asparagine and L-glutamine are the strongest amino acid stimuli and glass eels show thresholds of detection up to 10^{-9} mol l^{-1} (Crnjar *et al.*, 1992). Attraction to amino acids depends both on their concentration and the salinity of the water (Table 1). For example, D-alanine acts as an attractant in fresh water at concentrations of 10^{-9} M but acts as a repellent at higher concentrations (10^{-7} M) or if detected in sea water (Table 1) (Sola & Tongiorgi, 1998). Similarly, D-asparagine attracts glass eels in fresh water but has a repellent effect in sea water (Sola & Tongiorgi, 1998).

The behaviour of glass eels with respect to olfactory cues is complex. Glass eels are attracted by multiple chemical cues and these behavioural responses depend on multiple internal and external factors. For this reason, a comprehensive hypothesis on the odours or the combination of salinity gradients and odours that attract glass eels to estuaries has yet to be formulated. However, the morphological prominence and extreme sensitivity of their olfactory system, together with empirical evidence of attraction to odours, suggest that olfaction likely plays a central role in navigating coastal waters to find estuaries. Once the glass eels reach the estuaries, salinity and odours are likely to continue contributing to their orientation. However, at this stage of the migration, glass eels encounter fast-moving, turbulent tidal waters and the migratory strategy switches to mechanisms such as Selective Tidal Stream Transport (STST) and magnetic 'imprinting' of the currents. This facilitates their retention in estuaries as well as upstream migration in this new and challenging environment.

V. ARRIVAL AT ESTUARIES: PIGMENTATION, SELECTIVE TIDAL STREAM TRANSPORT (STST) AND MAGNETIC IMPRINTING

After the pelagic and coastal phases of their journey, glass eels eventually reach estuaries along the European and North African coast (Fig. 2A, Step 4). This is a critical step in their migration, as glass eels that reach estuaries transition into juveniles, and some swim upstream into fresh water. The period that glass eels spend in estuaries before moving into fresh water can last from a few weeks to years (until silvering) in the case of brackish water residents (Tzeng, Severin, & Wickström, 1997; Jessop *et al.*, 2008). The tendency of glass eels to migrate upstream is correlated with both their body condition (condition factor $K_n = 100\ M/M_{std}$, where M is the mass of an individual fish and M_{std} is the predicted mass of a fish of the same body length L, as calculated according to the $\log_{10}M$ *versus* $\log_{10}L$ logistic regression equation for the whole sample), as glass eels with higher K_n tend to prefer fresh water over salt water (Edeline *et al.*, 2006), and hormonal activity (Edeline *et al.*, 2005*a*). Furthermore, eels display facultative catadromy, as some never enter fresh water and some move multiple times between brackish and fresh water (Tsukamoto & Arai, 2001; Daverat *et al.*, 2006; Thibault *et al.*, 2007; Jessop *et al.*, 2008; Marohn *et al.*, 2013). In the context of facultative catadromy, the relationship between the migratory behaviour and body condition of glass eels is more complex. For European glass eels that remain in marine water, energy reserves (body condition) and standard metabolic rate are not always good predictors of their tendency to migrate (Liu *et al.*, 2019). Furthermore, marine glass eels sampled during the spring have lower energy stores and are less likely to migrate compared to those sampled in the autumn (Liu *et al.*, 2019). These multiple migratory strategies further complicate the understanding of their migratory behaviour at sea, in estuaries and in fresh waters.

Estuaries present conditions and physical properties that differ significantly from any other environment yet encountered by larvae or glass eels. Estuaries are characterized by freshwater input, dynamic changes in salinity, low visibility and abrupt variation in hydrodynamic conditions due to changes in freshwater outflow and tides. Extensive research has been conducted to understand the behaviour of glass eels in tidal estuaries and what environmental factors regulate this migratory step (Harrison *et al.*, 2014). It has been known for more than 50 years that the migratory behaviour of glass eels in tidal areas follows the alternation of ebbing and flooding tides, using a mechanism known as selective tidal stream transport (STST) (Creutzberg, 1961; McCleave & Kleckner, 1982; Gascuel, 1986; Wippelhauser & McCleave, 1987, 1988; Tankersley & Forward, Tankersley & Forward Jr, 2001; Beaulaton & Castelnaud, 2005). This is of particular importance considering that glass eels have relatively low critical swimming speeds (U_{crit}) that range between 10 and 12 cm/s, which they can sustain for only a short time (Langdon & Collins, 2000; Wuenschel & Able, 2008). Thus, glass eels rely on tidal flows to maximize the energetic efficiency of their migration upstream, moving upward in the water column during the flood tide and swimming down to the bottom during the ebb tide (Deelder, 1958; Jellyman, 1979; McCleave & Kleckner, 1982; Dou & Tsukamoto, 2003). This is supported by the observation that catches of glass eels in the upper layers of the water column occur mainly during the flood tide (Creutzberg, 1961; McCleave & Kleckner, 1982). Furthermore, observations confirm that glass eels tend to bury themselves in the sandy bottom during the ebb tide (Trancart *et al.*, 2012). Although the STST is accepted as one of the main mechanisms involved in the upstream migration of glass eels, there is evidence that their behaviour in tidal areas is more complex.

Sampling data of Australasian glass eels in the Waikato River in New Zealand suggest that glass eels again have an active phase of migration during the ebb tide, when they shoal and aggregate next to river shores (Jellyman & Lambert, 2003). This behaviour was integrated with the more classic concept of STST (involving mainly vertical movement), proposing that glass eels continue swimming during slack/early ebb tide, but along the margins of the river/stream (Harrison *et al.*, 2014). Sampling of *A. anguilla* glass eels in a large French estuary indicated that (at least in that area) only 15–19% migrated solely using STST, suggesting that active swimming might also play a role (Beaulaton & Castelnaud, 2005). This was deduced from peaks of abundance of glass eels both at the entrance of the estuary and further upstream, indicating a residency time of 20 days, and a migration speed of 3–4 km/day that could not be explained by STST alone (Beaulaton & Castelnaud, 2005). The migratory behaviour of glass eels in tidal estuaries is also associated with other factors such as location (Creutzberg, 1961; McCleave & Kleckner, 1982; Jellyman & Lambert, 2003), temperature (De Casamajor *et al.*, 2001; Laffaille, Caraguel, & Legault, 2007), light (Jellyman, 1979; De Casamajor, Bru, & Prouzet, 1999; Bureau Du Colombier *et al.*, 2007) and lunar cycle (De Casamajor *et al.*, 2001; Jellyman & Lambert, 2003). Clearly, the mechanisms by which glass eels migrate through estuaries and the specific cues that they use to find their way at this stage are complex.

Water currents (which also transport odours) caused by freshwater inputs and tides constitute one of the main directional cues for glass eels. Fish orient in moving water by an unconditioned response termed rheotaxis, which can be positive (the fish swims into the current) or negative (the fish swims with the current) (Arnold, 1974; Chapman *et al.*, 2011). Fish also use rheotaxis in tidal estuaries, as currents can be fast and in many cases visibility is low (Arnold, 1974). In such conditions, glass eels and other species display rheotaxis for two main tasks: upstream or downstream migration and upstream-oriented station-holding behaviour, which minimizes energy use in flowing water (Baker & Montgomery, 1999; Bolliet & Labonne, 2008) (Fig. 2B1 and B2).

In laboratory conditions, glass eels use rheotaxis to synchronize their swimming and orientation with the alternation of simulated tidal flows, showing rhythmic patterns of positive or negative rheotaxis mostly synchronized to the tidal period (Bolliet *et al.*, 2007). Furthermore, experiments show that glass eels are able to memorize the timing of the tidal flows (but with lower precision) after switching from alternating currents to constant conditions (Bolliet *et al.*, 2007). An analogous ability of glass eels to develop an endogenous rhythm entrained to the tidal phase was observed in American eels (*A. rostrata*), which showed swimming patterns synchronized with the tide when tested in the laboratory (Wippelhauser & McCleave, 1988). This ability to memorize the tide also plays a role in orientation with respect to Earth's magnetic field, as glass eels switch compass direction according to the tide when observed in a magnetic laboratory in the absence of flow (Cresci *et al.*, 2017). This mechanism has important implications for orientation in estuaries, where a magnetic compass alone would be of limited utility for upstream migration as streams continuously change direction with bends and meanders.

Thus, currents and tides are both important directional orientation cues in the estuary, determining the main directions towards which glass eels swim. Recent work indicates that this tidal-dependent rheotactic orientation also involves the eel's magnetic sense, seemingly through a process of magnetic 'imprinting' (Cresci *et al.*, 2019*a*). Specifically, glass eels collected from different estuaries, with associated ebbing and flooding tidal currents flowing in different cardinal directions, were observed in a magnetic laboratory. In the absence of currents, glass eels oriented against the magnetic direction of the prevailing tidal current occurring at their recruitment estuary (Cresci *et al.*, 2019*a*). These results suggest that glass eels' orientation against the tidal flow involves both rheotaxis and the sensing of magnetic fields (Fig. 2B1 and B2), as glass eels were able to form and retain a 'magnetic memory' of the direction of the tidal currents. This would allow them to orient with greater efficiency in moving water, especially when physical contact with the bottom and visual cues are lost in estuaries, where the water is turbid. This behaviour, together with rheotaxis, could help glass eels in station-holding behaviour in estuaries while undergoing the morphological and physiological changes to become elvers.

VI. RECOMMENDATIONS FOR FUTURE WORK

The literature on the migratory behaviour of glass eels highlights that many aspects of this complex process are not fully understood, and that additional research is required. Studies on orientation mechanisms linked to the lunar cycle are particularly challenging. With the alternation of the moon phases, the times and locations of moon rising and setting change, together with illumination intensity and features of the tides. Thus, lunar cycle-based orientation mechanisms are complex both for animals to use and for researchers to describe. With respect to glass eels, starting from the pelagic phase of their migration, more research is needed to describe the relationship between orientation and the lunar cycle. Specifically, *in situ* observations of lunar-related behaviour have so far only been conducted during daylight. Glass eels orient towards the moon during the new moon, when the moon is always above the horizon during the day, but below the horizon during the night. The opposite is true during full moon – the moon is below the line of the horizon during the day but above it at night. Future work should investigate orientation behaviour *in situ* at night, with particular focus on full moon nights. Furthermore, the full moon constitutes one of the phases of the lunar cycle during which electrical disturbances caused by the motion of the moon in its orbit occur. If electric fields are involved in lunar-related orientation, full moon nights could play an important role for oriented, directional swimming at sea.

Future work should thus investigate the possible mechanisms involved in lunar-related orientation. This could be done by reproducing in the laboratory electric fields with the same features as those associated with the moon's orbit, and testing the orientation of glass eels exposed to them. The role of lunar-related orientation in the recruitment of glass eels to estuaries could be investigated using biophysical models of dispersal integrated with empirical observations on lunar-related orientation behaviour.

Future work should also investigate the possible relationship and relative contributions of olfactory and magnetic cues during migration in coastal waters. This could be achieved under laboratory conditions by manipulating the direction of odour plumes in an artificially rotated magnetic field.

Another aspect of the migration of glass eels that needs more research is interindividual variability in orientation behaviour. Previous work on olfactory, rheotactic and magnetic cues highlighted that glass eels display noticeable variability in orientation responses, which might depend (among other factors) on different internal states, or so-called 'migratory urge'. Interindividual differences in European glass eels were observed during upstream migration in fresh water. Glass eels migrating through fish passages over barriers display 'leader/follower' internal states, which are associated with significant differences in neurogenesis ('leaders' have lower levels of transcription of synapse-related genes than 'followers') (Podgorniak *et al.*, 2016). Future work should use experiments involving two-choice maze trials (olfactory cues) or magnetic imprinting on subsets of 'migratory' and 'non-migratory' (proactive/reactive) individuals to investigate the role of the internal state of glass eels in their orientation behaviour.

VII. CONCLUSIONS

(1) Glass eels migrate from the pelagic water of the continental slope, passing through the continental shelf and coastal areas finally to reach brackish water estuaries. During their journey, glass eels encounter a multiplicity of environments, with dramatic differences in physical, chemical and biological features. This journey is extremely complex and glass eels need to rely on multiple orientation mechanisms in order to accomplish it.
(2) Based on an assessment of the literature describing the complexity of the behaviour of glass eels, and on recent findings on magnetic and lunar-related orientation, I propose that the migration of glass eels is a multi-step process, and that each step is driven by different orientation cues depending on the dominant physical and hydrodynamic conditions (Fig. 2). Thus, there is not one single behavioural strategy underlying the migration of glass eels, but rather they have the ability and plasticity to switch orientation mechanisms depending on which cues are available at each specific step.
(3) The switch between steps might require a transition phase during which glass eels adjust to the new environment and start exploiting new cues available for orientation. This ability allows glass eels to migrate through a broad variety of environments using a multi-step process involving a hierarchical succession of cues. As they move from the continental slope to the coast, glass eels use: (*i*) lunar and magnetic cues; (*ii*) chemical (odours and salinity) and magnetic cues; and finally (*iii*) rheotaxis (water currents), chemical cues and magnetic imprinting.

VIII. ACKNOWLEDGEMENTS

I thank Howard I. Browman, Anne Berit Skiftesvik and Caroline Durif for their guidance and support, and Josefina Olascoaga, Joseph E. Serafy, William Jones and Evan

D'Alessandro for their comments and suggestions. I thank Claire Paris for technical help with the research reviewed herein. I thank Romain Chaput and Tara Z. Baris for helpful and inspiring discussions. I thank Tom Quinn for the constructive comments. This research was supported by the Paris Lab at the Rosenstiel School of Marine and Atmospheric Science of the University of Miami, and by funds awarded to Howard I. Browman by the Norwegian Institute of Marine Research project 'Fine-scale interactions in the plankton' (project no. 81529) and the Research Council of Norway (project no. 234338). A.C. was supported by the U.S. National Science Foundation NSF-OCE 1459156 to Claire B. Paris and by the Norwegian Institute of Marine Research (project no. 81529 to Howard I. Browman).

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(*Received 3 December 2019; revised 20 April 2020; accepted 22 April 2020; published online 13 May 2020*)