

# The lunar compass of European glass eels (*Anguilla anguilla*) increases the probability that they recruit to North Sea coasts

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## Abstract

The European eel hatches in the Sargasso Sea and migrates across the Atlantic Ocean toward Europe. At the continental shelf, larvae metamorphose into glass eels and then recruit to coastal habitats and estuaries. Among other cues, glass eels orient in situ using lunar cues, but what role this lunar compass plays in their recruitment to the coast is unknown. To assess this, we incorporated empirical in situ observations of glass eel swimming and lunar-driven orientation into a biophysical advection model. We simulated dispersal of glass eels drifting with the North Atlantic Current to test the hypothesis that lunar-driven swimming and orientation behavior affects recruitment to North Sea coasts. Particles were released from the continental slope north of Scotland, an obligate passage for migrating eel larvae. Four numerical experiments were conducted: one with passive drift and three including glass eel swimming speeds (ranging from 3 to 12 cm/s) and lunar-driven orientation. With a speed of 3 cm/s, the lunar compass increased recruitment to the North Sea coasts of Southwestern Norway and Scotland by 34%–40%. Conversely, orientation behavior decreased recruitment to northern areas like Iceland (–46%), the Faroe Islands (–39%) and Northern Norway (–49%). Behavior affected the timing of recruitment to Southwestern Norway, causing peaks of abundance in May–June, but not to other regions. These results show that lunar-driven orientation and swimming behavior observed in glass eels substantially increases their recruitment to North Sea coasts. Results agree with the distribution of eel in northern Europe, which decreases in abundance with increasing latitude.

## KEYWORDS

biophysical model, dispersal, eel recruitment, European eel, fish orientation, migrations, Northern Europe

## 1 | INTRODUCTION

The European eel (*Anguilla anguilla*) migrates across the Atlantic Ocean twice in its life, from the spawning areas in the Sargasso Sea

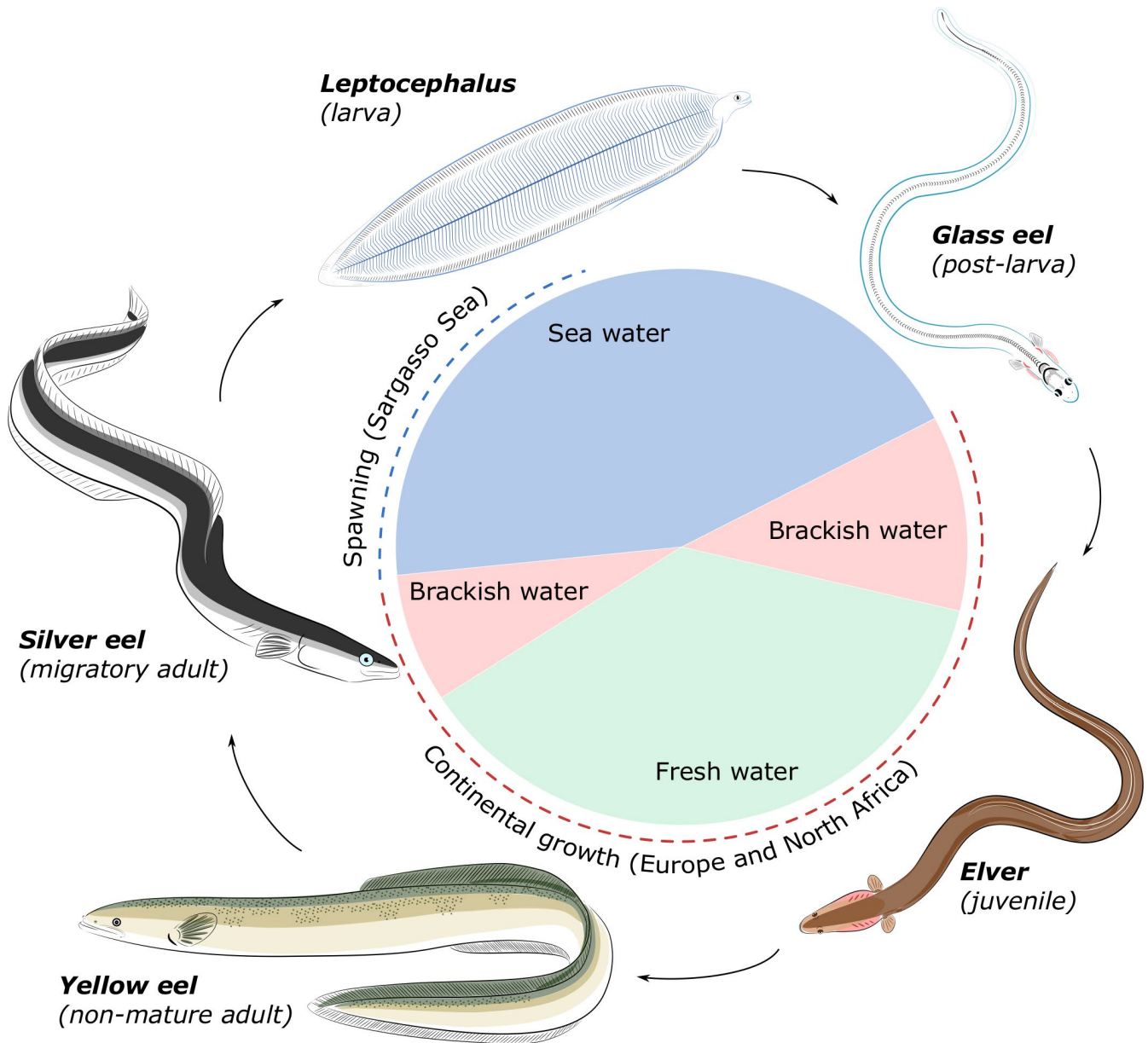
to the European and North African coasts as larvae and then back as adults (Johannes Schmidt, 1923). This species constitutes a single panmictic population (Als et al., 2011; Palm et al., 2009) inhabiting marine and freshwater habitats from Norway to Morocco. European

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eels hatch in the Sargasso Sea and drift with the Gulf Stream for >5,000 km as leptocephalus larvae (Bonhommeau et al., 2010; Tesch, 1977) until they reach the continental slope of Europe and North Africa (Figure 1). There, at the margins of the continental shelf, leptocephali metamorphose into transparent, post-larval glass eels (Tesch & Thorpe, 2003) (Figure 1). This stage differs significantly from the larval stage. Leptocephali larvae have a leaf-like shaped body, they grow in length with age, and they actively feed, while glass eels have a circular cross-body section, they stop eating until they recruit to the coast, and their length decreases with age (Deelder, 1952; Tesch, 1977). Thus, the glass eel stage is a fully

migratory, non-feeding stage during which eels cross the pelagic waters of the continental shelf to reach the coast. Once they reach coastal waters, glass eels recruit to estuaries, where some of them will start their upstream migration into freshwater as pigmented juveniles, called elvers (Tesch & Thorpe, 2003) (Figure 1), and some will remain marine or move between marine and brackish water (Bureau du Colombier et al., 2011; Daverat & Tomás, 2006; Marohn et al., 2013). Eels spend 5–30 years in freshwater as yellow eels, before becoming silver eels (Durif et al., 2009, 2020; Tesch, 1977), which then migrate back to the Sargasso Sea to spawn (Righton et al., 2016; J Schmidt, 1923).



**FIGURE 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, called elvers, they start the ascent into freshwater, 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. In this study, we focused on the glass eel stage. Artwork from Cresci, 2020

The European eel constitutes an important fishery in Europe (Starkie, 2003), and it has been exploited and farmed for thousands of years (Willem Dekker, 2003b, 2018). However, this species is now critically endangered [International Union for Conservation of Nature (IUCN)] and recruitment to freshwater has declined dramatically since the 1980s (Hilaire Drouineau et al., 2018; ICES, 2019b). In an effort to monitor the eel stock, models were developed to improve the assessment of recruitment of European glass eels to freshwater (Bornarel et al., 2018; Drouineau et al., 2016). However, the migratory routes and strategies that glass eels use to cross pelagic waters and reach the coast are still poorly understood. Better knowledge of these is needed to monitor and predict recruitment.

Glass eels have a complex orientation behavior based on a wide array of environmental cues that they use depending on the phase of their migration (Cresci, 2020). The most studied phase of the migration of glass eels is their entry into freshwater, as all the available monitoring data for glass eels comes from traps located upstream of the estuaries in fresh and brackish water (Dekker, 2002). All eel life stages possess an exceptionally sensitive olfactory system (Atta, 2013; Sola et al., 1993). When they are near the coast, glass eels are potentially guided by chemical cues, such as freshwater plumes transporting inland odors into estuaries (Tosi & Sola, 1993; Tosi, Spampinato, Sola, & Tongiorgi, 1989). Furthermore, glass eels orient using the magnetic field of the Earth (Cresci et al., 2017), which they use as a frame of reference to imprint a memory of tidal currents at the estuaries to facilitate position holding and upstream migration (Cresci, Durif, Paris, Shema, et al., 2019). The phase of glass eel migration about which the least is known is the pelagic marine phase during which they transition from leptocephali to glass eels at the continental slope and then cross the continental shelf to reach coastal waters.

Recent research described an orientation mechanism based on moon-related compass cues used by glass eels *in situ*, which could guide their pelagic migration (Cresci, Durif, Paris, Thompson, et al., 2019). Specifically, glass eels swim toward the direction of the moon azimuth at new moon during daytime, when the moon rises above the line of the horizon (Cresci, Durif, Paris, Thompson, et al., 2019). Further, even though this has not been empirically observed, glass eels were hypothesized to have the same behavior when the moon is above the horizon during full moon (which happens at night) (Cresci, Durif, Paris, Thompson, et al., 2019). During these two moon phases (new and full moon), the interaction of the moon with the Earth's magnetosphere and solar radiation causes the highest global-scale disturbances in electrical fields throughout the lunar cycle (Bevington, 2015; Kimura & Nakagawa, 2008). These have been discussed as potential cues involved in the sensitivity of glass eels to the lunar cycle (Cresci, Durif, Paris, Thompson, et al., 2019). Although the sensory mechanism involved is not clear, weak electric fields affect orientation behavior in juvenile eels (Zimmerman, & McCleave, 1975). Swimming toward the moon azimuth during these specific phases of the lunar cycle results in glass eels orienting, on average, in a southerly direction (Cresci, Durif, Paris, Thompson, et al., 2019). Nevertheless, while this link was

empirically observed, its role as a possible orientation mechanism guiding the recruiting population of glass eels from pelagic waters to the coast is still unclear.

Lagrangian biophysical models are commonly used to simulate advection and dispersal of early life stages of marine species (Bjorn Ådlandsvik et al., 2004; Lett et al., 2008; Paris et al., 2013; Sandvik et al., 2016; Swearer, et al., 2019; Vikebø et al., 2011). Larval dispersal in the ocean is governed by physical processes (ocean circulation and atmospheric forcing), but it is also influenced by biological processes (e.g., buoyancy; larval behavior), which can modify, often significantly, the trajectories of fish larvae and other planktonic organisms (Fiksen et al., 2007; Johnsen et al., 2014; Robins et al., 2013; Sandvik et al., 2020). Nevertheless, in the past three decades, more than half (53%) of studies on dispersal simulated it as pure passive transport with no behavioral control over either vertical position in the water column nor horizontal swimming (Swearer et al., 2019). Most studies that included larval behavior considered only vertical movement (fixed or variable through ontogeny) but did not incorporate horizontal swimming in simulations (Swearer et al., 2019).

In this context, observations have been made of the swimming and orientation behavior of fish larvae *in situ* by using divers following free-swimming larvae (Leis et al., 1996) and drifting *in situ* behavioral chambers (Drifting In Situ Chamber—DISC) (Paris et al., 2008). Examples of biophysical models of larval dispersal incorporating such empirically observed orientation and swimming behavior *in situ* come from simulations of transport of Mediterranean species (e.g., Sparidae) (Faillettaz et al., 2018). These models indicated that the empirically quantified larval behavior included in the model significantly modified the dispersal of these species to/from marine protected areas (Faillettaz et al., 2018). However, partially due to a lack of data on orientation and swimming behavior *in situ*, such an approach has never been used to simulate dispersal of the early life stages of fish living at high latitudes, including glass eels, which are nektonic organisms that actively swim across the continental shelf.

The recruitment of glass eels in the North Sea region has declined more severely than elsewhere in Europe (ICES, 2019b), and the northern North Sea constitutes one of the areas with the lowest number of sampling and monitoring stations (especially in Norway and Scotland) (ICES, 2019b). Specifically, the migratory routes of glass eels through the Shetland Channel into the North Sea have only been inferred, but never directly assessed through sampling programs at sea (Malcolm et al., 2010). Establishing such a sampling program is challenging due to the low abundance of glass eels in shelf water. Thus, more research is needed to describe the migratory pathways of glass eels in the North Sea.

In this study, we incorporated empirical *in situ* observations of glass eel swimming and lunar-driven orientation into a Lagrangian particle-tracking model for transport and dispersion (LADiM) (coupled with The Regional Ocean Modeling System (ROMS)) in order to assess how these behaviors influence dispersal of glass eels in northern Europe, from Iceland to the North Sea. We use several behavioral/biological input parameters for the model using data

**FIGURE 2** Main currents of northern Europe and the North Sea area, and configuration of the lunar-driven orientation behavior in the LADiM glass eels (*Anguilla anguilla*) advection model. **A:** The green area corresponds to the locations at which particles were released. The blue arrows are schematic representations of ocean currents. The main currents reaching the continental slope of northern Europe are the North Atlantic Current (NAC) and the shelf edge current, which both flow to the northeast and transport eel leptocephalus larvae toward the Shetland Channel. Downstream of the NAC, the Norwegian Coastal Current (NCC) flows to the north-northeast along the Norwegian coast toward the Arctic. The first part of the NCC originates in the Skagerrak, and it flows as a fast jet-like current to the North along the southwestern Norwegian coast (1–3 Sv transport; Mork, 1981). The North Sea circulation is cyclonic, with Atlantic water entering the basin from the north-northwest and flowing southward into the North Sea with a transport of close to 1.62 Sv (Turrell et al., 1992). The water that enters the North Sea through the English Channel (0.15 Sv transport; Bailly du Bois et al., 1995) flows north-eastward along the Netherlands, Germany and Denmark. **B:** In this model, particles were given the lunar compass orientation behavior that glass eels exhibit in situ. When the moon was above the horizon during new moon and full moon (Red arrows and fonts), simulated glass eels swam toward the average direction of the moon azimuth in the northern hemisphere (**South**). During 1st and 3rd quarter, and when the moon was below the horizon during full and new moon, glass eels had non-oriented swimming (Blue arrows and fonts)

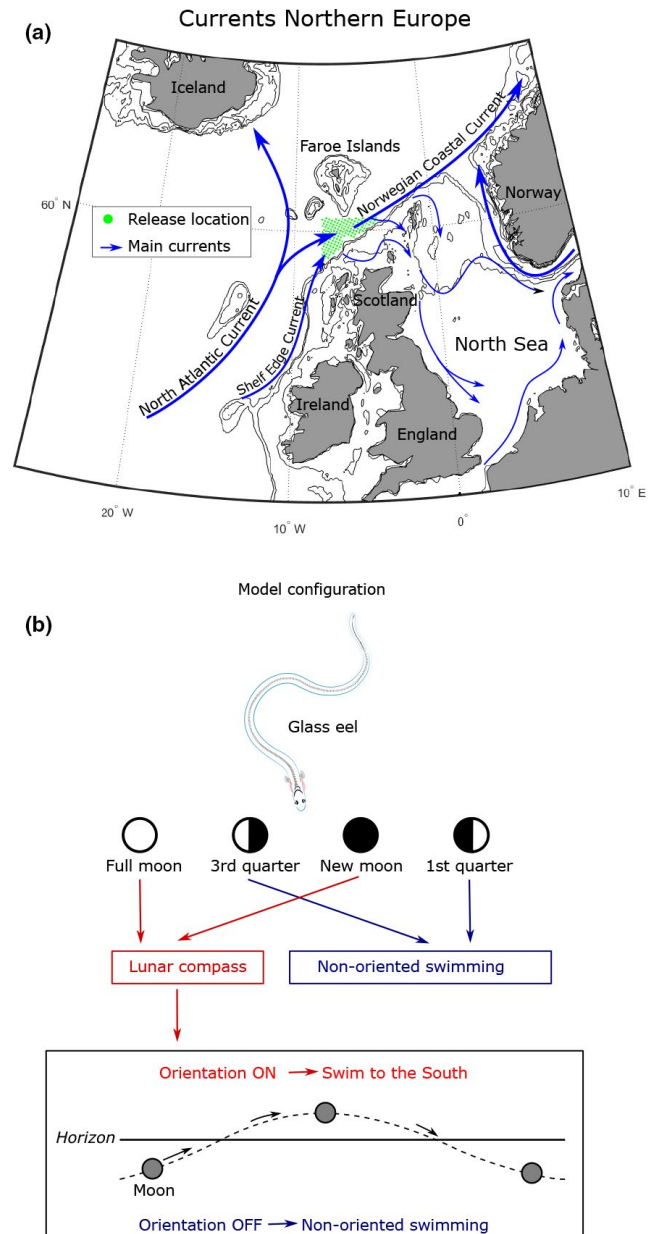
from behavioral experiments on glass eels performed in situ, in the North Sea (described in Cresci, Durif, Paris, Thompson, et al., 2019).

## 2 | METHODS

### 2.1 | Physical oceanography and topography of the study region

Particles were released from the edge of the continental shelf between northern Scotland and the Faroe Islands (Figure 2a), early during glass eels' recruitment season in northern Europe (January 1st–March 31st, for the year 2017). This area is upstream of the Faroe-Shetland Channel and corresponds to an obligate passage for eel leptocephalus larvae drifting with the North Atlantic current to reach the continental slope of the North Sea (Schmidt, 1927). We focused on the northern passage through the Shetland Channel with the objective of investigating glass eel migratory routes in northern Europe. From the Shetland area south of the Faroes, there is a large transport of Atlantic water into the North Sea, which is an order of magnitude higher than the transport through the English Channel (Bailly du Bois et al., 1995; Turrell et al., 1992). This difference in transport, coupled with the westerly winds dominating this area, causes most fish stocks recruiting to the North Sea to pass through the northern passage (Turrell, 1992). This is also considered to be the case for glass eels (Malcolm et al., 2010).

Once eel larvae arrive at the continental slope in the Faroe-Shetland Channel, they are presumed to metamorphose into glass eels and their landward migration begins (Schmidt, 1927). The depth of the



Faroe-Shetland Channel reaches >1,000 m in some areas. It rises rapidly over the continental shelf, where it ranges between 20 and 200 m in the North Sea, with the exception of the Norwegian Trench, which reaches 500 m deep. The North Sea area is governed by a cyclonic circulation, with intrusions of the North Atlantic Current (NAC) and European Shelf water from the northwest (Winther & Johannessen, 2006) (Figure 2a). This Atlantic water flows to the south and then turns east-southeast toward the Norwegian Trench (Figure 2a). More to the south, east of the English Channel, coastal water flows to the northeast, following the coasts of the Netherlands and Denmark up to the Norwegian Trench (Sundby et al., 2017) (a diagram of the currents with associated transport values is shown in Figure 2a).

In this study, we considered all of the coasts downstream of the main currents transporting glass eels in Northern Europe (e.g., NAC, North Sea currents) as potential recruitment areas. Specifically, the coastal areas included in this study are as follows: *Northern Norway*

(N.Nor.), Southwestern Norway (Sw. Nor.), Denmark and Skagerrak (Denm.), Southern North Sea (Germany and most of Netherlands) (S. North Sea), East-Southeast England (E-SE Eng.), Scotland (Scot.), Faroe (Far.), and Iceland (Ice.) (Figure 3). Annual recruitment of glass eels occurs in all of these coastal areas (ICES, 2019b).

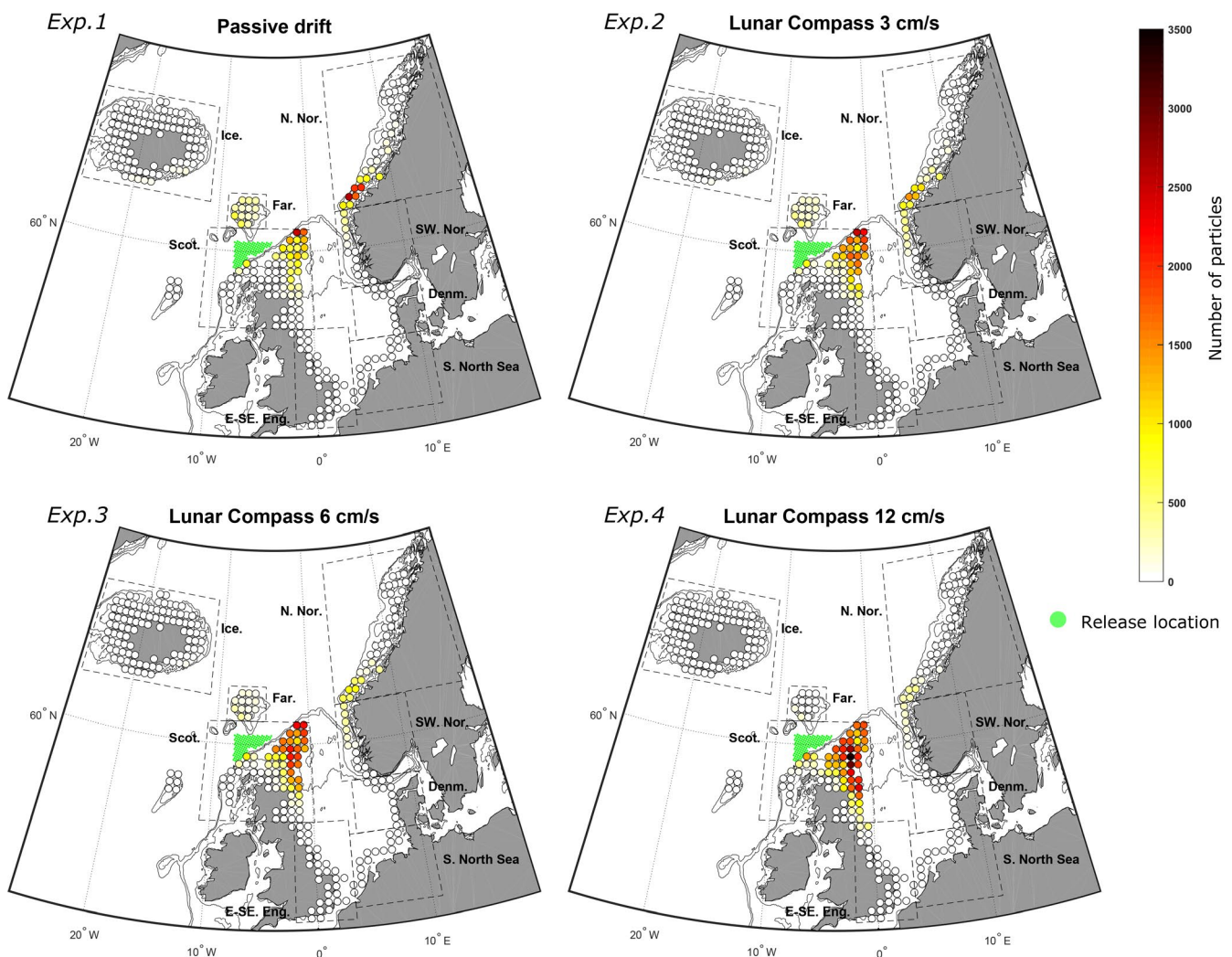
## 2.2 | Hydrodynamic model

Currents and hydrography are provided by a one-way nested system consisting of a coarse scale ocean model covering the North Sea, Nordic Seas, and Barents Sea, and a higher resolution model system, NorKyst800, covering the Norwegian coast (Albretsen et al., 2011; Mykssvoll et al., 2018). Both models are based on the Regional Ocean Modeling System (ROMS, [www.myroms.org](http://www.myroms.org); Haidvogel et al., 2008;

Shchepetkin & McWilliams, 2005), which is a free-surface, terrain-following, hydrostatic, primitive equations ocean model. The horizontal quadratic grid cell size is 4 x 4km in the outer domain and 800 x 800 m in the inner domain along the Norwegian coast. Realistic forcing of the ocean model from atmosphere, tides, and rivers is included as described by Asplin et al. (2014) and Johnsen et al. (2014). The model results consist of hourly values of 3-dimensional currents, salinity, and temperature and served as input to the glass eel dispersion model.

## 2.3 | Glass eel dispersion model and design of the simulation

The glass eel advection model is based on the Lagrangian Advection and Diffusion Model (LADiM) (Bjørn Ådlandsvik, 2020).



**FIGURE 3** Simulated glass eels (*Anguilla anguilla*) recruiting to the coasts of northern Europe, inside and outside the North Sea. The four maps summarize the results of the four different experiments conducted in this study: Exp. 1 = passive drift; Exp. 2 = Lunar compass with swimming speed of 3 cm/s; Exp. 3 = Lunar compass with swimming speed of 6 cm/s; Exp. 4 = Lunar compass with swimming speed of 12 cm/s. The green area is the particle release area. Circles are centers of polygons of 25 x 25 nautical miles adjacent to the coast. Recruitment polygons are grouped in macro-regions, which are illustrated by dashed line rectangles. The macro-regions are: Denm, Denmark and the Skagerrak; E-SE England, East-southeast England; Far, Faroe; Ice, Iceland; N. Nor, Northern Norway; S. North Sea, Southern North Sea; Scot, Scotland; SW. Nor., Southwestern Norway

For this work, the LADiM model was implemented with biological parameters assessed through behavioral experiments conducted on glass eels in situ using the *Lunar\_eel* plugin, version 1.2 (Sævik, 2020).

### 2.3.1 | Time window

Particles were released daily from January 1, to March 31, 2017, and their dispersal was simulated until June 30, 2017. This particle release period was selected following otolith microstructure analysis on glass eels arriving to the coast of Sweden, which estimated that they metamorphose from leptocephali to glass eels at the continental slope during the month of January (Wang & Tzeng, 2000). In addition, based on sampling cruises conducted in the early 1900s (Schmidt, 1906), it was estimated that metamorphosing larvae arrive at the continental slope north of Scotland in the months of January–February (Creutzberg, 1961; Heusden, 1943). Glass eel dispersal was run until June 31st because by the summer (July–August) glass eels have already reached the coasts of the North Sea, undertaken pigmentation into elver, and started the upstream migration into freshwater (Deelder, 1952; ICES, 2020; Vøllestad & Jonsson, 1988).

### 2.3.2 | Depth

Particles were released uniformly between 0 and 20 m depth and were allowed to move vertically (randomly) within the upper 20 m. This depth range was selected because glass eels move in relatively shallow water over the continental shelf. Compared to the younger leptocephali larvae, which move between 35–600 m and perform daily vertical migration (Tesch, 1980), older glass eels move mostly in the upper 20 m of the water column. In the Swedish sound of the Baltic, glass eels were sampled with drop traps at 0.5–1.5 m (Westerberg, 1998). Observations in the North Sea along the Dutch coast and in the Wadden Sea show that glass eels can be sampled with ring trawls at 0–8 m (Creutzberg, 1961). Sampling of the closely related American glass eels (*A. rostrata*) in the Gulf of St Lawrence, Atlantic coast of Canada shows that they were captured at the surface using horizontal surface tows (Dutil et al., 2009).

Glass eels and elvers are known to undertake some vertical movement according to light and tides (Creutzberg, 1961; Deelder, 1952). However, these movements are mostly in the upper 10 m of the water column and the only information available on vertical movement of glass eels in situ come from coastal areas and traps in freshwater. Thus, no data are available on the vertical swimming behavior glass eels throughout the day in pelagic shelf water. For these reasons, we implemented the model with horizontal swimming behavior—no vertical movement was simulated—and kept the particles from the surface to 20 m deep during the drift.

### 2.3.3 | Orientation and swimming behavior

In order to simulate realistic behavior of migrating glass eels, we implemented the model with experimental data on compass orientation direction from Cresci, Durif, Paris, Thompson, et al., 2019. Glass eels tested in situ in the North Sea display orientation behavior that is linked to the lunar cycle. Specifically, glass eels orient toward the direction of the moon azimuth during new moon during the day, and during full moon during the night, when the moon is above the line of the horizon (Cresci, Durif, Paris, Thompson, et al., 2019). This behavior causes glass eels to orient on average to the south (Cresci, Durif, Paris, Thompson, et al., 2019).

We implemented the lunar-based compass in the model by setting the particles to orient only during new and full moon and only when the moon was above the horizon (Figure 2b). When the moon falls below the line of the horizon and when the lunar cycle switches phase (to first and third quarter), glass eels display non-oriented swimming, which was simulated by slow random movements (corresponding to a diffusion coefficient of 1). The number of hours during which the moon is above the horizon during new and full moon changes depending on the day and the time of the year. Data on the position of the moon with respect to the horizon for the period of the simulation were obtained from <https://www.timeanddate.com/moon/>. During these specific conditions of the lunar cycle (new moon and full moon when the moon is above the horizon), particles oriented toward the south (mean direction = 180°). During 1st and 3rd quarter, and during full/new moon when the moon was below the horizon, particles had non-oriented swimming (Figure 2b). Overall, the proportion of time of the whole simulation during which particles had oriented swimming was 23%.

### 2.3.4 | Swimming speed and experimental design

We designed the simulation considering several swimming speeds that glass eels could potentially have when migrating over the continental shelf. We also ran the model without behavior (passive drift) to have a control experiment as a reference against which to assess the effects of behavior on dispersal. We ran four different simulations (experiments) of dispersal differing in presence/absence of orientation and swimming speed:

- **Exp. 1**—Passive drift with no orientation and swimming behavior—**Control**
- **Exp. 2**—Lunar-based compass orientation with oriented swimming speed of **3 cm/s**—*Speed from experiments in situ with drifting chambers (DISC)*
- **Exp. 3**—Lunar-based compass orientation with oriented swimming speed of **6 cm/s**— $\frac{1}{2}$  *critical speed (Ucrit)*
- **Exp. 4**—Lunar-based compass orientation with oriented swimming speed of **12 cm/s**—*Approximate Ucrit of glass eels from literature*

The swimming speed of 3 cm/s for the **Exp. 2** is the median swimming speed that glass eels have in situ when swimming in drifting in situ chambers (DISC) in the North Sea (Cresci, Durif, Paris, Thompson, et al., 2019). This swimming speed is much lower than the swimming speeds that glass eels can sustain in the laboratory (Langdon & Collins, 2000), and it could be a “cruising” speed of European glass eels over the shelf. The swimming speeds of 6 cm/s and 12 cm/s of **Exp. 3** and **Exp. 4** are approximate estimates of half of the Ucrit (critical speed—prolonged swimming where velocity is gradually increased at set intervals until the point of complete fatigue; Brett, 1964) and the Ucrit of glass eels, respectively. Wuenschel and Able (2008) estimated the Ucrit of closely related American glass eels (*A. rostrata*) entering estuaries and concluded that it ranges between 13–19 cm/s (Wuenschel & Able, 2008), which is slightly higher than the speed in **Exp. 4**. The same authors explain that glass eels are likely to sustain 50% of that swimming speed (close to 6 cm/s; **Exp. 3**) for over 24 hr. In tropical reef fish larvae near settlement (11 families), there is a strong relationship between the Ucrit and the in situ speed, with the latter being approximately 50% of Ucrit (Leis & Fisher, 2006). Applying this to glass eels, considering a Ucrit of 13–19 cm/s, and maintaining in situ speeds that are 50% of Ucrit, glass eels would swim at 6.5–9.5 cm/s and move 3–8 km/day (Wuenschel & Able, 2008). This supports the idea that glass eels could migrate at swimming speeds close to 6 cm/s, which is the speed used in **Exp. 3**. The swimming speed of 12 cm/s used in **Exp. 4** is probably an overestimate of the possible cruising speed of glass eels, and it was selected for sensitivity analysis of the effect of speed on dispersal. This speed is close to the Ucrit of 13–19 cm/s of glass eels of *A. rostrata*, and it is slightly lower than the speed of 15 cm/s that European glass eels can sustain for 60 min (Langdon & Collins, 2000; Tsukamoto et al., 1975).

### 2.3.5 | Potential recruitment areas

The objective of this study is to test the hypothesis that lunar compass-based orientation affects the recruitment of migrating glass eels to the coasts of the North Sea. To quantify recruitment, we defined potential recruitment areas as polygons of 25 x 25 nautical miles seaward starting from the coastline (drawn in ArcGIS). This is motivated by the fact that glass eels have an extremely developed olfactory sense (Sola et al., 1993), and they are attracted by freshwater and inland odors emanating from the coast (Sola, 1995; Tosi & Sola, 1993). Thus, when they reach coastal water and detect these odors, they could switch behavior from lunar compass to olfactory-driven orientation and follow brackish plumes at the surface coming from streams and rivers, which are numerous in the North Sea (Farmer & Freeland, 1983; Radach & Pätsch, 2007). A total of 310 polygons were created following the entire coastline downstream of the particle release area, from Iceland to the Netherlands (Figure 3). When a particle enters one of the polygons, this is considered as a potential recruitment. Particles were allowed to keep drifting after entering a polygon, as glass eels might not recruit to that specific

area but continue migrating. Thus, each particle could cross more than one polygon and enter more than one macro-region.

## 2.4 | Quantification of abundance and timing of recruitment

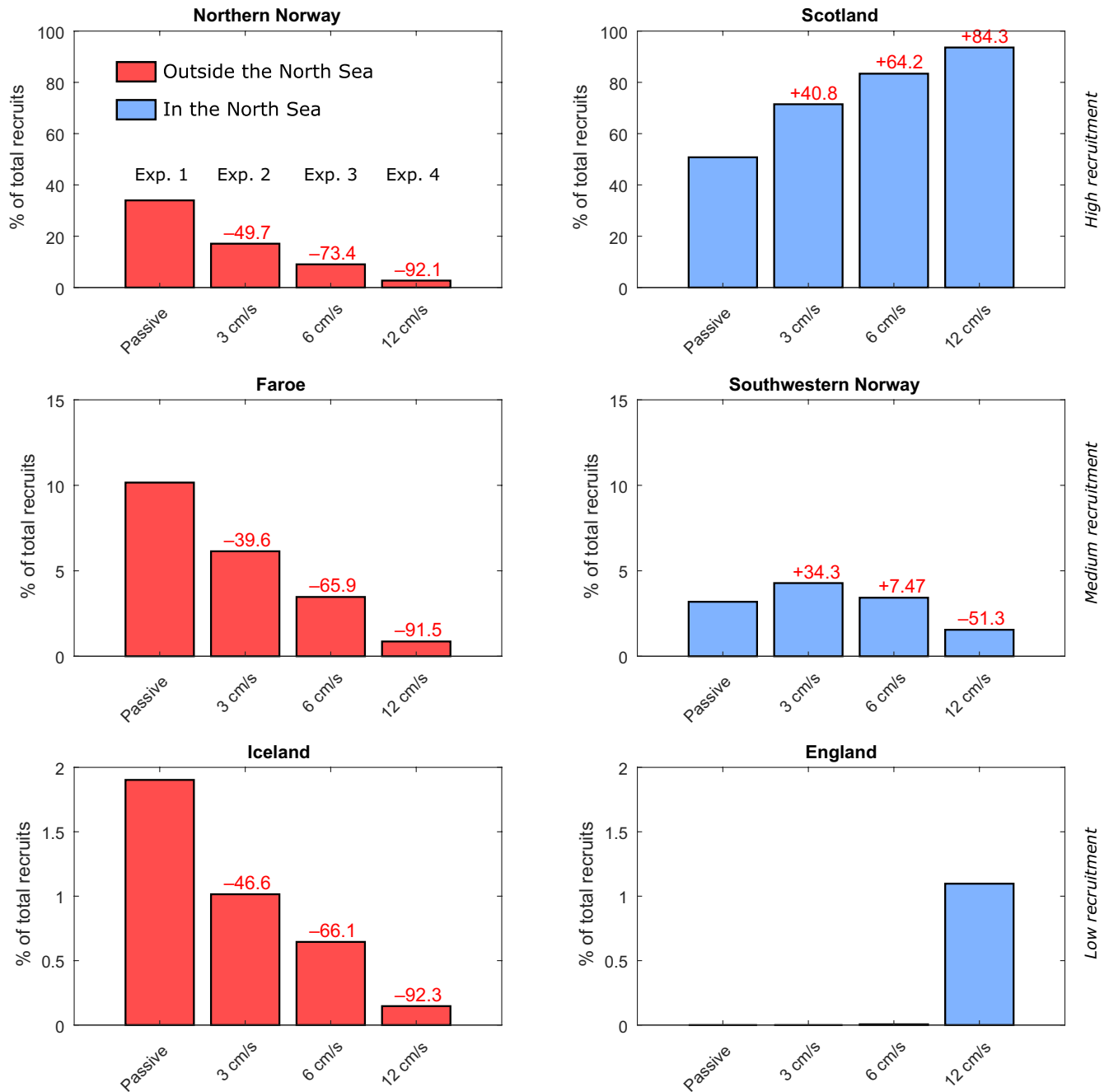
Macro-regions were further grouped according to their location with respect to the North Sea (*inside* the North Sea; *outside* the North Sea; Figure 4). For the quantification of potential recruits, we counted the cumulative abundance, during the whole recruitment period, of particles passing through all of the potential recruitment polygons of each macro-region. For each of the 4 experiments, we then normalized the cumulative abundance of recruits in each macro-region with respect to the total number of recruiting glass eels to all macro-regions, and we expressed it as a percentage of total recruitment (Figure 4). Because the objective of the study is to evaluate possible effects of swimming and orientation behavior on recruitment, we calculated the variation in recruitment in the experiments resulting from changes in behavior (**Exp. 2,3,4**) as compared to the experiment with passive drift (**Exp. 1—passive drift**) in the same macro-region. This comparison is expressed as relative increase/decrease of the percentage of total recruits in the experiments with behavior compared to the experiment with passive drift in each one of the macro-regions (Figure 4).

The timing of recruitment was also calculated for each one of the macro-regions, from March 1st until June 31st (Figure 5a), which is the main recruitment period of glass eels in the North Sea (Creutzberg, 1961; Deelder, 1952; Durif et al., 2008; Heusden, 1943; ICES, 2020; Skiftesvik, 1984). We report the time series of the percentage of total recruits in each of the experiments (Figure 5a). Time series are from daily estimates of recruits in each macro-region and for each experiment. Values of total daily recruits (for each experiment in each macro-region) were normalized with respect to the total daily recruits in all macro-regions (% of total daily recruits; Figure 5a). Furthermore, because the hypothesis being tested is that behavior affects recruitment, we calculated the difference in the percentage of total daily recruits between passive drift and each of the experiments that included behavior, for each macro-region (Figure 5b). To highlight possible patterns in the timing of recruitment with respect to the lunar cycle, we displayed the time series overlapped with new and full moon phases (Figure 5).

## 3 | RESULTS

### 3.1 | Recruitment

Lunar compass orientation behavior increased the amount of simulated glass eels recruiting to the coasts inside the North Sea compared to simple passive drift (Table 1; Figures 3–4). This increase of recruiting glass eels to the North Sea coasts was consistent for all the macro-regions—*England, Southwestern Norway, and Scotland*—where

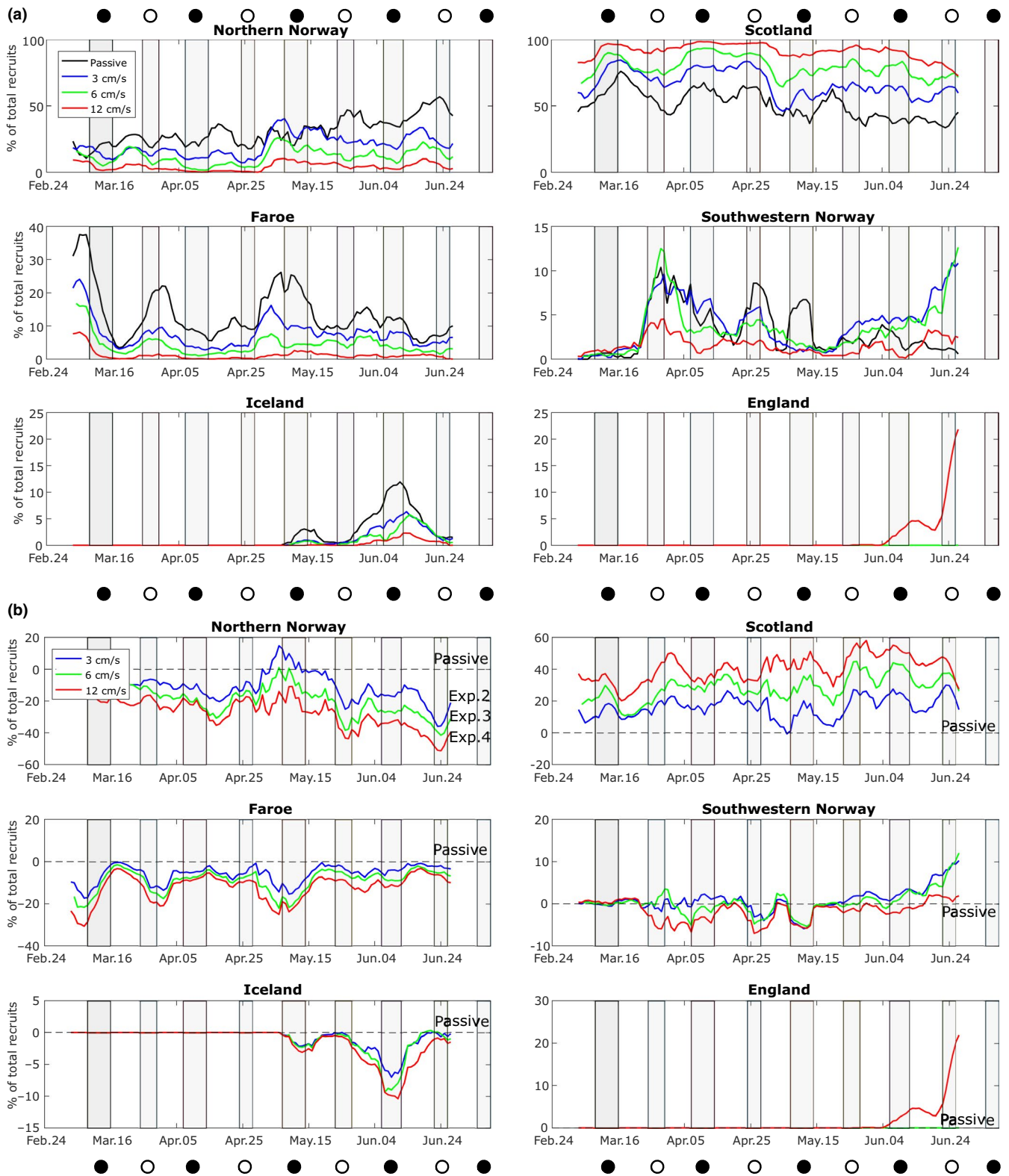


**FIGURE 4** Cumulative recruitment of glass eels (*Anguilla anguilla*) to each macro-region and each experiment. Each plot shows the cumulative abundance through the recruitment period (March 1st and June 31st), for one macro-region and for all four experiments. Only macro-regions where recruitment occurred are considered in this analysis. The cumulative abundance is normalized with respect to the total number of recruiting glass eels (to all macro-regions) in each experiment, and it is expressed as a percentage (%). Red bars show percentage of total recruits in macro-regions **outside the North Sea**; Blue bars show percentage of total recruits in macro-regions **inside the North Sea**. Red numbers on top of the bars of Exp. 2, 3, and 4 show the percentage of variation of recruitment in the same macro-region with respect to the experiment with passive drift (Exp. 1). Exp. 1 = passive drift; Exp. 2 = Lunar compass with swimming speed of 3 cm/s; Exp. 3 = Lunar compass with swimming speed of 6 cm/s; Exp. 4 = Lunar compass with swimming speed of 12 cm/s. The labels for Exp. 1, 2, 3, and 4 are displayed only in the first subplot for clarity, but apply to the bars of all subplots

recruitment occurred, except for the fastest swimming glass eels entering *Southwestern Norway* (Figure 4). The other macro-regions in the North Sea (*Denmark, Southern North Sea*) did not have any recruitment between March 1st and June 31st (Figure 3). Conversely, the model shows that, compared to passive drift, oriented swimming

linked to the lunar compass leads to a substantial decrease (Table 1) in number of recruits in *Northern Norway, Faroe Islands, and Iceland*, which are outside the North Sea (Figure 3). Macro-regions differed in overall proportion of total recruits, which was highest in *Scotland* (Table 1).





**FIGURE 5** Time series of recruitment of simulated glass eels (*Anguilla anguilla*) during the recruitment season. Each plot shows the time series of recruitment to one macro-region. Lines are color-coded with respect to the experiment. White and black circles, as well as light gray rectangles, show the period of full or new moon. Only macro-regions in which recruitment occurred are considered in this analysis. The abundance of recruits is normalized with respect to the total daily number of recruiting glass eels (to all macro-regions) in each experiment, and it is expressed as a percentage (%). **A:** Time series of percentage of total recruits. **B:** Time series of the difference in percentage of total recruits between experiments with behavior (Exp. 2,3,4) and the experiment with passive drift (Exp. 1 –horizontal dashed line), for each macro-region. Exp. 1 = passive drift; Exp. 2 = Lunar compass with swimming speed of 3 cm/s; Exp. 3 = Lunar compass with swimming speed of 6 cm/s; Exp. 4 = Lunar compass with swimming speed of 12 cm/s

**TABLE 1** Proportion of glass eels (*Anguilla anguilla*) recruiting to each macro-region for each experiment

	High recruitment		Medium recruitment		Low recruitment	
	N. Norway (%)	Scotland (%)	Faroe (%)	SW. Norway (%)	Iceland (%)	England (%)
	Outside North Sea	Inside North Sea	Outside North Sea	Inside North Sea	Outside North Sea	Inside North Sea
Exp. 1 (Passive Drift)	34.0	50.8	10.2	3.2	1.9	0
Exp. 2 (3 cm/s)	17.1	71.5	6.1	4.3	1.0	0
Exp. 3 (6 cm/s)	9.1	83.4	3.5	3.4	0.6	0
Exp. 4 (12 cm/s)	2.7	93.6	0.9	1.5	0.1	1.1

Note: The proportions are reported as percentage of total recruits in the simulation.

The impact of the lunar compass on recruitment varied considerably depending on swimming speed (Figure 4). In Exp. 2, with the lowest swimming speed of 3 cm/s, recruitment decreased 40 to 50% compared to passive drift in all of the regions outside the North Sea (Figure 4). Exp. 3 shows an additional decrease of the number of recruits relative to Exp. 2 in the regions outside the North Sea, with a 66%–73% decrease in recruitment compared to passive drift (Figure 4). The lowest recruitment outside the North Sea was in Exp. 4, which had the highest swimming speed used in this study of 12 cm/s (Ucrit glass eels) (Figure 4). Exp. 4 shows a decrease in recruitment of > 90% compared to passive drift in all the regions outside the North Sea (Figure 4). This trend was opposite for the macro-regions inside the North Sea, except for *Southwestern Norway*. *Scotland* had a strong increase (41%) in the number of recruiting glass eels in Exp. 2 compared to passive drift, and it reached an increase in recruitment of 64% in Exp. 3 and 84% in Exp. 4 (Figure 4). In *Southwestern Norway*, recruitment increased only when dispersal was simulated with slow swimming speeds (Exp. 2,3). Specifically, recruitment increased by 34% compared to passive drift with the slowest swimming speed in Exp. 2, but it had a lower increase (7%) in Exp. 3 (Figure 4). *Southwestern Norway* had 51% more recruiting eels in Exp. 4 (highest swimming speed) compared to passive drift (Figure 4). In *England*, recruitment occurred only in Exp. 4 (Figure 4).

### 3.2 | Timing of recruitment

Swimming and orientation behavior results in lower recruitment in all the macro-regions outside the North Sea throughout the whole recruitment period compared to the experiment with passive drift (Figure 5a, b). Conversely, in *Scotland* (in the North Sea), recruitment was consistently higher than that observed with passive drift throughout the recruitment season when behavior was included (Figure 5a, b).

*Southwestern Norway* experienced more complex patterns of recruitment depending on the month. In this region, recruitment was the lowest in Exp. 4 throughout almost the entire season (Figure 5a, b). In this region, recruitment peaked at the end of March through early April, although it rose again toward the end of this period in

Exp. 2 and 3 (Figure 5a). However, later in the season, experiments with swimming speeds of 3 and 6 cm/s (Exp. 2 and 3) showed increasing trends of recruitment abundance in *Southwestern Norway* from the end of May through the end of June (Figure 5a, b). *Iceland* did not receive any recruits until May, but experienced peaks of abundance in June (Figure 5a). Similarly, glass eels reached *England* during early June and only in the experiment with the highest swimming speed (Figure 5a, b).

With the exception of *Southwestern Norway* and *England*, increasing swimming speed and orientation behavior affected the overall amount of recruiting eels, but did not substantially affect the timing of arrival to the coast: time series of recruitment follows similar evolution patterns in all of the experiments that included behavior (Figure 5a, b).

## 4 | DISCUSSION

### 4.1 | Comparing the results of the model with the distribution of the European eel

In this study, simulations of dispersal were performed using a glass eel biophysical advection model coupled with empirical observations of glass eel behavior in situ. These simulations reveal that geographical trends in recruitment abundance in northern Europe can be considerably affected by glass eel swimming and orientation behavior and that swimming speed is likely to play a central role in this process.

According to Schmidt (1909), who conducted the first comprehensive study on the distribution of the European eel, the habitat of this species extends from Cape North in Northern Norway to the coasts of North Africa (Johs Schmidt, 1909). Nevertheless, the abundance of eels across this continent-wide area is not uniform; it varies with latitude and longitude due to the temperature preferences of the species and the features of the North Atlantic Ocean circulation (Durif et al., 2011; Kettle et al., 2008). The results reported in this study show that lunar-related swimming and orientation behavior substantially reduces the proportion of glass eels recruiting to the North (*Iceland*, *Northern Norway* and *Faroe*) and increases glass

eels recruitment to the North Sea coasts. In this model, oriented swimming was not continuous throughout the period of the simulation but occurred only for some hours on full and new moon days (Figure 2b). These results show that the alternation of moon-guided oriented swimming and non-oriented swimming, timed by the movement of the moon at the horizon, significantly influences the dispersal of glass eels. Moreover, the outcome of the model is consistent with several studies on the distribution of glass and adult eels, which both decline in numbers at higher latitudes—from the North Sea toward the Arctic (Willem Dekker, 2003a; Johs Schmidt, 1909).

In the model, with the speeds of 3–6 cm/s in Exp. 2, the proportion of glass eels recruiting to *Northern Norway* decreased, but it increased in *Southwestern Norway* compared to passive drift (Figure 4). These results suggest that the lunar compass orientation could help reduce the chances for glass eels to drift north with the Norwegian Coastal Current toward the Arctic (Figure 2a), thereby increasing recruitment to the North Sea coast of Norway. This is consistent with the actual distribution of the European eel in Norway.

Along the Norwegian coast, eels are more abundant in marine and continental waters in the southwest of the country and become less numerous in the northern part of Norway toward Cape North (Bergersen & Klemetsen, 1988; Davidsen et al., 2011; Willem Dekker, 2003a). Schmidt identified the latitude of Trondheim at 63° N in Norway as the northern limit after which eel abundance starts to decline (Johs Schmidt, 1909). In our model, *Northern Norway* received an overall higher proportion of glass eel recruits (Table 1) compared to *Southwestern Norway*. In the model, the higher abundance of glass eels in Northern Norway is caused by the predominant flow of the NAC transporting particles toward the northeast and of the NCC (Norwegian Coastal Current) (Figure 2a), which is a fast jet current flowing to the north-northeast along the Norwegian coast (Mork, 1981; Winther & Johannessen, 2006; Figure 2a). However, what is not accounted for in the model is the probability of survival and successful glass eel recruitment. In *Northern Norway*, there are less suitable freshwater habitats for eels, and water temperatures are at the lower limit of the range of thermal preferences for this species (Willem Dekker, 2003a; Sadler, 1979). Thus, it is possible that an overall higher number of glass eels drifts to *Northern Norway* compared to *Southwestern Norway*, but that a higher proportion of these do not successfully recruit to freshwater (Durif et al., 2008). This difference in recruitment between northern and southern Norway in our simulations was highest if glass eel dispersal was simulated as passive drift, but it substantially reduced with swimming speeds of 3 and 6 cm/s (Table 1). Because glass eels are known to be more abundant in *Southwestern Norway*, these results support the idea that recruitment of glass eels to the coasts of the North Sea is a process involving both advection with currents and oriented swimming behavior.

The model showed that potential recruitment of glass eels occurred in both the *Faroe Islands* and *Iceland*, in all the simulations. Some glass eels recruit far north to Icelandic freshwater, where genetic hybrids between the European eel and the American eel (*A. rostrata*) are found (Avisé et al., 1990; Kuroki et al., 2008). The results

from our model show that 2% of simulated glass eels recruited to *Iceland* and that this proportion decreases significantly (to < 1%) when orientation behavior is included (Figures 3 and 4). This outcome might be driven by the ocean circulation pattern in this area, as part of the NAC separates from the main flow upstream of the Shetland Channel and moves to the north (toward *Faroe* and *Iceland*). Thus, the lunar compass could also function as a mechanism that lowers the probability that glass eels are transported toward *Iceland*.

According to the model, the highest potential recruitment occurred in *Scotland*, independent of the swimming speed. The geographical proximity of the Scottish coast to the NAC and the Shetland Channel, with currents flowing close the Scottish coasts into the North Sea (Figure 2a), is probably a key factor for the high potential recruitment to this area. Currently, no sampling of glass eels off the coast has been conducted in *Scotland*, and the only evidence of the presence of eels in the country comes from data on yellow eel in freshwater collected by the Scottish Fisheries Coordination Centre (SFCC) (Malcolm et al., 2010). Most of the eel sampling in Scottish freshwaters was conducted by electrofishing, for which eels were not the target species. Therefore, the abundance and distribution of eels in Scottish freshwater are probably underestimated (Malcolm et al., 2010). It is believed that glass eels are numerous and widespread across all of the marine areas around the Scottish coast, with higher concentrations in the north of the country (Malcolm et al., 2010). Glass eel trawl sampling at sea should be conducted in this area to reveal the importance of the Scottish coast as a recruitment area.

The model showed that throughout the recruitment period, no glass eels reached *England* in any experiment except Exp. 4, which had the highest swimming speed (12 cm/s) (Figure 4). These results suggest that recruitment to the eastern and south-eastern coasts of England is supplied by glass eels entering the North Sea through the English Channel. Nevertheless, the North Sea is characterized by a cyclonic circulation, and reaching the eastern coasts of *England* might be challenging for glass eels entering the basin through the English Channel. In England, eels are more abundant in the west of the country compared to the east-northeast (ICES, 2019a). In the eastern British areas of Northumbria and Humber, there is no commercial fishery on glass eels and eel biomass is among the lowest in the country (ICES, 2019a). Overall, our results showing no or low arrival of glass eels in eastern *England*, the cyclonic oceanography of the North Sea, and the historical data on British eel stocks, all indicate that eel recruitment to eastern *England* is generally low.

Our results show that glass eels entering the North Sea through the northern passage do not recruit to the Netherlands, Germany, or Denmark. Eels are abundant in these countries, which have major freshwater bodies and coastal brackish water areas where glass eels are monitored (W Dekker, 2000; Willem Dekker, 2003a; ICES, 2019b). Thus, recruitment in these areas is most likely supplied by glass eels arriving through the English Channel. Considering the results of this study, we propose that recruitment of glass eels in the North Sea occurs through two main routes supplying different countries: 1) a northern route from the northwest of the North

Sea supplying recruitment to *Scotland*, *Southwestern Norway*, and possibly (with low numbers) north east *England* and a second route through the English Channel supplying the *Southern North Sea*, *Denmark*, and east-southeast *England*.

Our model did not resolve how recruitment to the Skagerrak occurs. In this area, glass eels are abundant, and they recruit to southern Norway and the Baltic Sea (Durif & Skiftesvik, 2018). The abundant recruitment to the Skagerrak is probably linked to the convergence of currents in this area coming from both the north-west and the south of the North Sea. Future work using biophysical models should investigate the migratory routes that glass eels use to reach the Skagerrak.

## 4.2 | Timing of recruitment

Data on recruitment of glass eels to Europe come from commercial fisheries and monitoring programs conducted using sampling stations/traps mostly located in fresh and brackish water (Willem Dekker, 2003a; ICES, 2019b). Thus, it is difficult to make comparisons between the timing of recruitment of glass eels to the coast from our model and that indicated by the sampling for juvenile elvers migrating in freshwater, as these two events are sequential but not necessarily entirely consistent in terms of numbers.

In *Southwestern Norway*, juvenile and adult silver eels have been monitored since the 1970s. Data from the Imsa station show that most elvers ascend the river starting in June (C. M. F. Durif et al., 2008; Leif Asbjørn Vøllestad & Jonsson, 1986). From our model (which was run for the year 2017), recruitment of glass eels to *Southwestern Norway* starts from the end of February but it peaks from the end of March to the beginning of April (Figure 5a). Throughout this period, recruitment is highest in the experiment with a swimming speed of 3 cm/s (Figure 5b), which is the lowest speed used in this study. This timing agrees with catches of glass eels at the estuaries around the Austevoll archipelago (Bergen area), where glass eels arrive from the beginning of March through the beginning of June (Skiftesvik, 1984; Cresci, Skiftesvik, Durif and Browman—personal observations from sampling performed in 2015, 2016 and 2017). It is possible that the glass eels recruiting to *Southwestern Norway* between March and April might be the first ones to ascend the rivers in June at the elver stage, as is the case at Imsa. Moreover, our model shows that peaks of recruitment in *Southwestern Norway* occur from the end of May through the end of June (Figure 5b) only in the experiments with realistic swimming speeds (Exp. 2–3). Glass eels that recruit to the southwest of Norway at the end of spring (end of May to the end of June) could be those ascending the rivers as elvers during July, as most elvers migrate upstream in the Imsa River from June through the end of July (Durif et al., 2008; ICES, 2020).

Compared to *Southwestern Norway*, the time series of recruitment of both *Northern Norway* and *Scotland* have different characteristics. In these areas, recruitment appears to be less variable over time (Figure 5). *Scotland* received recruiting glass eels throughout

the recruitment period, from the beginning of March until the end of June (Figure 5). Interestingly, recruitment to *Scotland* steadily decreases over time if dispersal is simulated as only passive drift, but it remains stable in the simulations with swimming and orientation behavior (Figure 5). Conversely, the experiment with passive drift shows a slow and steady increase of recruitment over time in *Northern Norway*, but it remains relatively stable in the experiments that included swimming and orientation behavior (Figure 5a). These results suggest that behavior plays a role in determining arrival of glass eels to these areas throughout the recruitment season.

Recruitment of eel larvae to the continental shelf, and of glass eels to the estuaries, occurs in “waves” (Desaunay & Guerault, 1997; ICES, 2020), which are possibly linked to different spawning events in the Sargasso Sea (there are genetic differences between the individuals in these waves) (Pujolar et al., 2006). Our results on the timing of recruitment to *Scotland* and *Northern Norway* could indicate that recruitment of glass eels in these areas is likely to occur steadily over the recruitment season, presenting less pronounced trends compared to other regions. This may be related to the close proximity of these two areas to the major currents (NAC, NCC) that transport eel larvae to northern Europe, as glass eel recruitment depends on fluctuations in the circulation of the North Atlantic (Durif et al., 2011; Kettle et al., 2008).

In the model, recruitment peaks in the *Faroe* Islands occurred during the beginning of March, April, and May (Figure 5a). Peaks of abundance in the *Faroe* Islands were particularly pronounced in the simulation with passive drift but flattened when behavior was included in the model, suggesting that these peaks are mainly caused by circulation features of the NAC. Additionally, analogous to *Northern Norway*, scenarios that included behavior showed that recruitment in the *Faroe* Islands was lower than the experiment with passive drift throughout the recruitment period (Figure 5b). The same happens in *Iceland*, with the difference that glass eels reach the island only in May (Figure 5).

## 4.3 | Conclusions and future directions

The results of this study demonstrate that the lunar-driven orientation and swimming behavior of glass eels significantly influences their recruitment to the North Sea coasts. Swimming for some hours of the day (when the moon is above the horizon), toward the average direction of the moon azimuth (south), at cruising speeds that are much lower than those that glass eels reach in the laboratory (e.g., Ucrit), substantially increases their chances to recruit to the coasts of the North Sea and potentially further into the Baltic. These results represent an example of the importance of incorporating empirical data on in situ orientation and swimming behavior in biophysical models of dispersal, as these can strongly affect the trajectory, and fate, of simulated early life stages of fish.

Future work should simulate dispersal in the North Sea of glass eels coming through the English Channel using biophysical models integrated with empirical observations of behavior. Finally, the same approach should be applied to investigate glass eel recruitment to

southern Europe and explore how lunar-related orientation influences the proportion of eels entering through narrow passages such as the Strait of Gibraltar and the English Channel.

## 5 | COMPETING INTERESTS

The authors declare no competing interests.

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### AUTHOR CONTRIBUTION

A.C. designed the study, analyzed the data, interpreted the results, and wrote the manuscript. A.D.S. designed the study, run the model, and wrote the manuscript. P.N.S. designed the study, designed the model, and wrote the manuscript. B. Å. designed the study, designed the model, and wrote the manuscript. M.J.O. analyzed the data, interpreted the results, and wrote the manuscript. P.M. analyzed the data and wrote the manuscript. C.M.F.D. designed the study, interpreted the results, and wrote the manuscript. A.B.S. designed the study, interpreted the data, wrote the paper, and funded the research. H.I.B. designed the study, interpreted the data, wrote the paper, and funded the research. F.V. designed the study, interpreted the data, wrote the paper, and funded the research.

### DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

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