



How fast can the European eel (*Anguilla anguilla*) larvae cross the Atlantic Ocean?

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ABSTRACT

The migration duration of European eel (*Anguilla anguilla*) larvae (leptocephali) from the spawning areas in the Sargasso Sea to the European continental shelf remains highly controversial, with estimates varying from 6 months to more than 2 yr. We estimated the fastest migration period and the shortest distance travelled by eel larvae by simulating Lagrangian particles released in the Sargasso Sea and by simulating a range of larval behaviours (fixed-depth drift, vertical diurnal migration and active-depth selection to maximize current velocity). This enabled us to compute (i) a passive drift speed, and (ii) a hypothetical swimming speed needed for European eel larvae to cross the Atlantic in 6 months (i.e., the migration duration estimated from otolith daily growth increments). Our results show that the minimum travel time for an eel larva that is passively drifting was 10 months and 3 days. Active behaviours (vertical diurnal migration

and rheotaxis) paradoxically increased the migration period. We found that for leptocephali to cross the Atlantic Ocean in 6 months, they would need to swim a minimum of 3.4 body lengths per second for 8200 km. No larvae have been observed with such swimming capabilities. These results provide evidence that leptocephali cannot cross the Atlantic in 6 months.

Key words: *Anguilla*, fractals, Gulf Stream, Lagrangian modelling, leptocephali, migration duration, Sargasso Sea

INTRODUCTION

The European eel (*Anguilla anguilla*) is a catadromous fish with an extremely long ocean migration route. Larvae are conveyed by warm ocean currents more than 6000 km, from the Sargasso Sea in the east Atlantic to the African and European shelf (from Mauritania to the Polar Circle; Schmidt, 1923).

The current worldwide decline in eel populations has been well documented (Anonymous, 2003) and, with its current low level of abundance, the European eel has been listed in the Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007). The decline in the European eel population since the early 1980s is no doubt the combined effect of several interacting factors, which are difficult to disentangle: anthropogenic activities such as overfishing (Dekker, 2004), habitat loss and degradation (McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006) and increasing stress in the freshwater stage due to parasites and diseases (e.g., Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005) and in the oceanic stage due to unfavourable oceanic conditions (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008).

The oceanic larval phase of European eels is of primary importance to understand eel ecology. There has been a long history of ecological studies dealing with marine life stages of this species (Dekker, 1998). As for most fish species, the major source of mortality occurs during the larval stage (Hjort, 1914). Moreover, this oceanic phase determines the dispersion over the

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Received 17 September 2008

Revised version accepted 11 May 2009

coastal regions and the freshwater habitats. The migration duration is certainly one of the most critical and controversial features of the oceanic larva migration. The migration duration defines the age at which larvae settle as well as the spatial distribution of larvae as they arrive on European and African coasts. It also conditions our ability to understand how recruitment is linked to environmental fluctuations. This is critical in a context where major changes in oceanic conditions are known to impact fish populations (Beaugrand and Reid, 2003; Lehodey *et al.*, 2006). Eel recruitment data have been compared to environmental factors such as large-scale oceanic and climate indices (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008; Kettle *et al.*, 2008). Friedland *et al.* (2007) suggested that fluctuations in latitude of the 22.5°C isotherm, which is a useful proxy for the northern limit of eel-spawning area, may be linked to fluctuations of retention processes within the Sargasso Sea gyre that affect both spawning location and transport of the leptocephali out of the Sargasso Sea. Kettle *et al.* (2008) showed a negative relationship between the state of the North Atlantic Oscillation (Hurrell, 1995) and glass eel catches in Europe. They suggested that this relationship might be linked to the larval survival in and migration from the Sargasso Sea spawning location. Primary production and sea-temperature fluctuations in eel-spawning area have also been shown to be related to glass eel recruitment (Knights, 2003; Bonhommeau *et al.*, 2008). All these studies used recruitment indices based on glass eel arrivals. Because oceanic environmental conditions are suspected to impact eel larvae several months before their arrival at the European shelf, linking environmental descriptors to glass eel recruitment necessitates a time lag to account for migration duration. Results still remain conditioned by the hypotheses made about migration duration, e.g., a 1-yr lag for Friedland *et al.* (2007) and a 2.5–3-yr lag for Knights (2003) and Bonhommeau *et al.* (2008).

Uncertainties about migration duration arise mainly due the difficulty in observing eel larvae during their oceanic stage. During the 70 yr following the discovery of eel-spawning locations (Schmidt, 1922, 1923), the migration duration of the European eel was speculated to be between 2 and 3 yr. This assumption was grounded on growth curves of eel larvae. However, since the development of otolith microstructure analysis, estimates of the migration duration have changed. Sampling 423 eel larvae from the Netherlands to Morocco, Lecomte-Finiger (1992) estimated that the migration duration (migration + metamorphosis into glass eels) took between 191 and 276 days

(about 6–9 months) for glass eels caught in Portugal and UK, respectively. E. Réveillac, R. Lecomte-Finiger and E. Feunteun (unpublished data) estimated a similar migration duration, i.e., 6–7 months (71–88 days for metamorphosis). Wang and Tzeng (2000) estimated the age of European glass eels as between 14 and 16 months (98 days for metamorphosis). Arai *et al.* (2000) and Kuroki *et al.* (2008) found intermediate migration durations of 7–9 and 11 months (58 days for metamorphosis), respectively. Several hypotheses have been advanced to explain such short migration duration, such as the active and/or oriented migration hypothesis (Lecomte-Finiger, 1992, 1994). It has been shown how ocean general circulation models may provide insights to better grasp this trans-oceanic migration. Using Lagrangian simulations, Kettle and Haines (2006) found that over a 4-yr period (1993–1996) the minimum migration duration of the European eel larvae was approximately 2 yr.

Here we follow Kettle and Haines (2006) and attempt to learn about the migration duration of the European eel by performing Lagrangian simulations. However, our approach differs from Kettle and Haines (2006) in three ways. First, we did not investigate mean pathways and migration durations. Rather, we focussed our analysis on the hypothesis testing: *Can eel larvae cross the Atlantic Ocean in 6 months?* To test this, we focussed on the fastest Lagrangian particles drifting between the Sargasso Sea and the European shelf, to establish a minimum bound for the migration duration. Secondly, we used two different high-resolution general circulation model configurations: Drakkar and Mercator. Simulations were possible over a period of 45 yr with the Drakkar model. The use of two different configurations enabled us to compare results and test the accuracy of the Lagrangian simulations. Thirdly, we relaxed the hypothesis of strict passive drift by testing different active, larval behaviours of vertical migration. Our simulations attempted to determine a minimum bound for the migration duration, across larval behaviours. Clearly, a very large number of different particle behaviours need to be tested to find the true minimum bound for migration duration; however, this is impossible in practice. Hence, we limited our analysis to three scenarios that are mostly designed to explore how an active behaviour of vertical migration may affect the migration duration: (i) particles drifting at fixed-depth as in Kettle and Haines (2006); (ii) particles undergoing a vertical diurnal migration between 300 and 50 m as observed in the wild (Castonguay and McCleave, 1987); and (iii) particles drifting at the depth where the velocity of currents (whatever the direction) is the highest.

In so doing, we calculated the passive drift speed of the fastest particles. In addition, we addressed the question of whether active behaviour enables particles to reach the European shelf more quickly. We also estimated the minimum swimming speed required for particles to cross the Atlantic Ocean in 6 months.

MATERIALS AND METHODS

Circulation models

Lagrangian simulations were performed using two different oceanic model configurations (Drakkar and Mercator). Both models are based on the NEMOOPA (Nucleus for European Modelling of the Ocean/Océan Parallélisé) numerical code (Madec, 2008). In comparison with the model used by Kettle and Haines (2006), these general ocean circulation models have better vertical resolution and longer integration periods.

Of the two models used, the Drakkar model (<http://www.ifremer.fr/lpo/drakkar>) covers the longest period (1958–2004), and allowed us to address the interannual variability of trajectories. The model configuration is global. It uses the ORCA025 grid (a tripolar grid with a $1/4^\circ$ horizontal grid resolution at the equator). The configuration is described by Barnier *et al.* (2006) who demonstrated its good performance in representing strong currents and eddy variability, even compared with higher resolution models. The water column is divided into 46 levels, with grid spacing ranging from 6 m near the surface to 250 m at the bottom. The simulation was run using atmospheric data (a blend of satellite products and ERA40 6-h winds, temperature and humidity). The Drakkar model is a fully prognostic model, which means that it does not use assimilation data (neither satellite altimetry nor in situ temperature or salinity), and therefore can be substantially different from observations in some areas. Fortunately, those biases are less pronounced in the subtropical gyre, which is our region of interest, than in the subpolar regions (Tréguier *et al.*, 2005). For the purposes of our Atlantic analysis we used velocities only for the area ranging from -82 to 6°E and from 10 to 60°N . As the observed depth of leptocephal ranges from -50 to -300 m (e.g., Castonguay and McCleave, 1987), we reduced the oceanic model to the top 24 levels (-3 to -989 m). To avoid the early spin-up phase of the model, we used the period 1960–2004 of the simulation. Circulation fields were time-mean archived every 5 days, which was the best possible compromise in terms of disk usage between the length of the simu-

lation and the need for a fair sampling of the most energetic scales of variability present in the model.

The ocean velocity fields provided by the Mercator project (<http://www.mercator-ocean.fr>) were from the PSY1v2 analysis, which covers the period 1992–2002 (the whole available period of this model). Velocity fields are archived every day. The horizontal grid resolution is $1/3^\circ$ at the equator. The geographical extension of this simulation is from 20°S to 70°N in the Atlantic. It encompasses 43 vertical levels from surface to -5000 m (the vertical resolution is from 12 m at the surface, to 200 m at the bottom). The model was forced by altimetry and in situ data, which are fully described in the MERA-11 general scientific paper (Greiner *et al.*, 2006). The area covered by the model has been reduced to -98 to 20°E , and to 20°S to 70°N and the depth was limited to the first 16 levels (-453 m).

Lagrangian simulation designs

This study attempted to determine a minimum bound for the migration duration for particles drifting from the Sargasso Sea to the European shelf.

In all scenarios (defined hereafter as a combination of a model, Drakkar and Mercator, with one of the three behaviours tested for the particles), particles were released in the Sargasso Sea every 15 days (constrained by computational power) throughout the year. It is well known that the spawning season occurs during late winter and spring (e.g., McCleave *et al.*, 1987) but particles were released throughout the year to explore the widest possible range of trajectories and increase the chance to approach the minimum bound for the migration duration.

Particles were tracked over a 1.5-yr period, which is long enough to capture the fastest particle trajectory. We used the Ariane tool developed by B. Blanke and N. Grima (Laboratoire de Physique des Océans, CNRS-IFREMER-IRD-UBO, Brest, France, freely available at <http://www.univ-brest.fr/lpo/ariane>). This FORTRAN code is dedicated to the computation of 3D streamlines in a given velocity field (as the output of an Ocean General Circulation Model) and subsequent water mass analyses. The Ariane tool takes advantage of 'C' grids used for horizontal discretization in numerical codes such as NEMOOPA to analytically compute trajectories from model outputs. This algorithm calculates true trajectories for a given stationary velocity field. The Ariane tool has been used successfully in several studies to derive relevant information about basin-scale or global-scale circulation patterns (e.g., Blanke and Raynaud, 1997; Blanke

et al., 1999, 2001). Instead of analysing water masses (water particles) with the Ariane tool, we used it to track eel larvae, defined here as a particle.

In the Drakkar configuration, drifters were released within each model grid cell, i.e., each $1/4^\circ$ and each of the 24 fixed-depth levels in an area enclosing the assumed spawning area of eels in the Sargasso Sea (Fig. 1). A total of 1 972 608 particles were thus released every 2 weeks, each yr (one particle released every 0.25° over the area bounded by $75\text{--}50^\circ\text{W}$ and $22\text{--}30^\circ\text{N}$, for each of the 24 depth levels). To reduce simulation time, we restricted the whole available period (1958–2004) to three contrasting periods, defined by different states of the North Atlantic Oscillation (NAO; Hurrell, 1995). This provided an overview of different oceanic conditions. The Atlantic Ocean general circulation can be contrasted in terms of strength and/or latitude of the Gulf Stream (Taylor and Stephens, 1998; Curry and McCartney, 2001). Winter North Atlantic Oscillation is a good proxy to estimate the position and strength of the North Atlantic currents. Curry and McCartney (2001) showed that the potential energy anomaly (i.e., the strength of the Gulf Stream) is well correlated to NAO. The same applies for the latitude of the Gulf Stream measured by the Gulf Stream Index (Taylor and Stephens, 1998). Kettle *et al.* (2008) showed that the migration of eel larvae may be linked to the NAO by a larval migration failure in the Sargasso Sea due to vertical density stratification and food restrictions. The selected periods were thus 1960–1964 (mean NAO Index = -1.7), 1973–1977 (0.9), and 1986–1999 (1.6). We then tested the relationships between arrival success, minimum migration duration and the NAO index.

In the Mercator configuration, drifters were released at each model grid, i.e., each $1/3^\circ$ and each of

the 16 depth levels over the whole period available (1992–2002) in the same area as in the Drakkar model. A total of 691 104 particles were released each year (one particle released every $1/3^\circ$ from 75 to 50°W and from 22 to 30°N , for each of the 16 depth levels and twice a month).

For both model configurations, three different particles behaviours were tested in Lagrangian simulations to explore how an active behaviour of vertical migration may affect the migration duration. We first assumed a fixed-depth drift for all particles released at each vertical level of the reduced model. This experiment corresponded to the hypothesis tested in Kettle and Haines (2006). In a second experiment, a vertical diurnal migration was implemented. Particles flip every 12 h from 300 to 50 m, as described in Castonguay and McCleave (1987). This experiment mimics the behaviour of eel larvae in the wild: leptocephalus collections have been shown to have a diurnal migration depending on their length (Castonguay and McCleave, 1987). Until the length of 7 mm, they are uniformly distributed over the 300-m upper layers (Schmidt, 1922; Schoth and Tesch, 1984; Castonguay and McCleave, 1987). When the larvae are larger, a diurnal vertical migration is observed from 300 m in the daytime to 50 m at night (Schmidt, 1922; Castonguay and McCleave, 1987; McCleave, 1993; McCleave *et al.*, 1998). Although these different behaviours during the earliest life stages of eel leptocephali and afterwards have been observed, we chose to implement the daily flipping from 300 to 50 m as soon as particles were released. In a third experiment, at each time step, particles flipped from their current depth layer to the one with the fastest current speed, independent of the direction of the current. Although this active behaviour

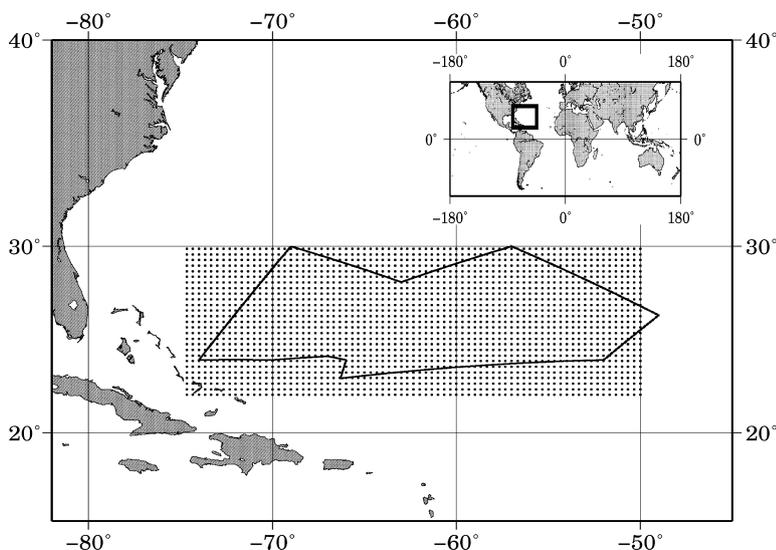


Figure 1. Map of the initial positions for the Lagrangian simulations using the Mercator model (i.e., each $1/3^\circ$). The European eel-spawning area is charted by a black polygon (from Fig. 2 in McCleave *et al.*, 1987). The initial positions using the Drakkar model have the same bounds as Mercator but are each set at $1/4^\circ$.

might appear to have only limited biological meaning, it is grounded on the known positive rheotaxis behaviour of glass eels, a mechanism whereby they will turn to face an oncoming current (Bertin, 1956; Bolliet *et al.*, 2007). Here we assumed that leptocephali might use the same ability to drift and choose the fastest currents. But it is worth noting that this third experiment remains mainly a way to explore a wider range of possible trajectories, in order to increase the chance of finding a minimum bound for the migration duration. Clearly, a more optimal experiment would have consisted in covering all the possible particles trajectories corresponding to particles that could change depth randomly, but such an experiment proved impossible to run in practice because of limits in computational power.

Analysis

Finishing line for the trajectories. Output files of Lagrangian simulations include position (longitude, latitude, depth) and time for each particle. Particles were considered to have ‘succeeded’ in their migration when crossing the 20°W meridian, whatever the latitude. This finishing line is further east than the 25°W chosen by Kettle and Haines (2006). As the aim of the study was to estimate the migration duration of the fastest particle, the finishing line had to be as close as possible to the effective arrival area of eel larvae to compare it with current estimates. However, 20°W is a reasonable limit, as longitudes higher than 20°W correspond to continental slope, which is not as well resolved by the physical model as the open ocean. Moreover, Lagrangian simulations are unable to represent tidal transport of eel larvae when they reach the shelves. Knowing the position and time of each particle, we calculated the distance covered by each particle reaching the finishing line and the migration duration. The mean drift speed v_i for each particle i was estimated by the expression:

$$v_i = \frac{d_i}{t_i} \quad (1)$$

where d_i is the distance covered by the particle i that succeeded in crossing the 20°W meridian and t_i is the corresponding time taken to travel that distance.

Statistical analysis. To assess the impact of oceanic conditions on the migration duration and success, we analysed the link between the number of particles that succeeded in reaching 20°W and the intensity of three large-scale oceanic indices averaged over the years of drift: the winter NAO (Hurrell, 1995), the Gulf Stream Index (GSI, Taylor and Stephens, 1998), and

the Potential Energy Anomalies (PEA, Curry and McCartney, 2001). The correlations were checked after removing trends and autocorrelation from the time series. Indeed, procedures for statistical testing of the correlation between the series of oceanic indices and migration features must take into account the autocorrelation and trends in the time series because these might result in an artificial increase in the statistical significance of the correlation test (Pyper and Peterman, 1998). We thus first-differenced the different time-series and then calculated the Pearson’s correlation coefficient between the time-series as recommended in Pyper and Peterman (1998).

Fractal dimension to characterize trajectories. To reach the shelf as quickly as possible, a particle has both to be in the fastest current and to cover the shortest distance. When a particle drifts at a depth with the fastest current velocity, particles with the most ‘linear’ trajectory will cover the shortest distance and then have the shortest migration duration. For each trajectory, we used the fractal dimension as a synthetic index to characterize its linearity. The fractal dimension is a measure of how successive positions of particles fill the plane where they are located. It characterizes the drift, from linear (lower fractal dimension) to chaotic (higher fractal dimension). The fractal dimension was calculated with the function `fdim` from the package `FDIM` (de Pison Ascacibar *et al.*, 2007) of R Cran-project (R Development Core Team, 2007).

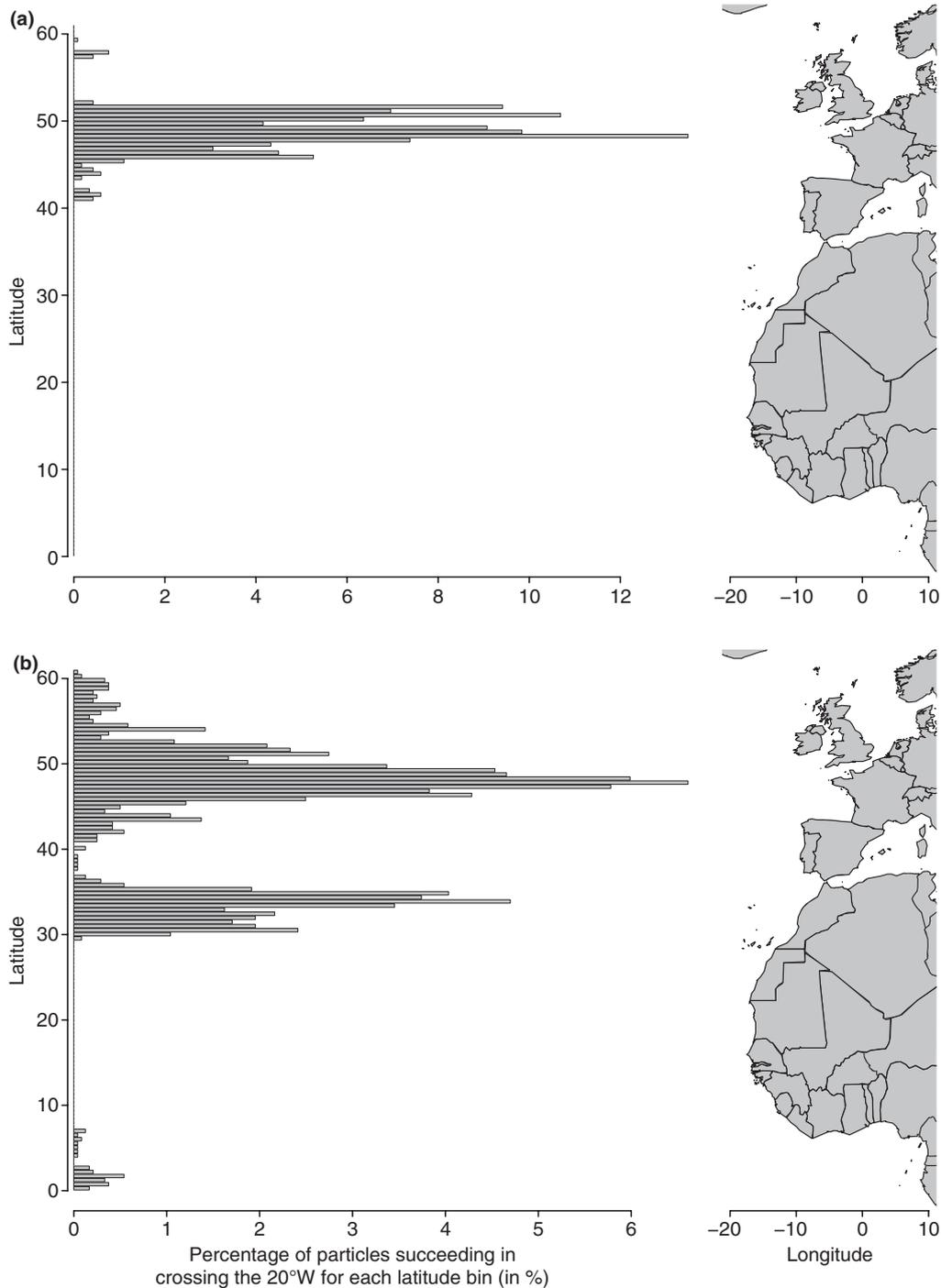
RESULTS

Simulations are consistent with previous knowledge

The results of Lagrangian simulations are consistent with observations of larval departure and arrival areas. With the Drakkar model, after a migration duration of 1.5 yr, the distribution of particles at 20°W was spread across 40°N and 55°N, with a peak at 50°N (Fig. 2a). Similar patterns were observed with the Mercator model, but another peak appeared in North Africa (30–35°N), as found by Kettle and Haines (2006) (Fig. 2b). In the Drakkar model, the Azores Current is weakly represented, which explains the low proportion of particles arriving at Morocco.

Most arriving particles were seeded in the departure area located in the Western Sargasso Sea (75–65°W and 22–30°N; Fig. 3 for the Drakkar model). When arriving in the East Atlantic the depth range of particles crossing the 20°W meridian ranged from –400 m to the surface for both models (Fig. 4a,b). The shape of the distribution of these depths has a mode at –200 m depth, for both models, with another peak at

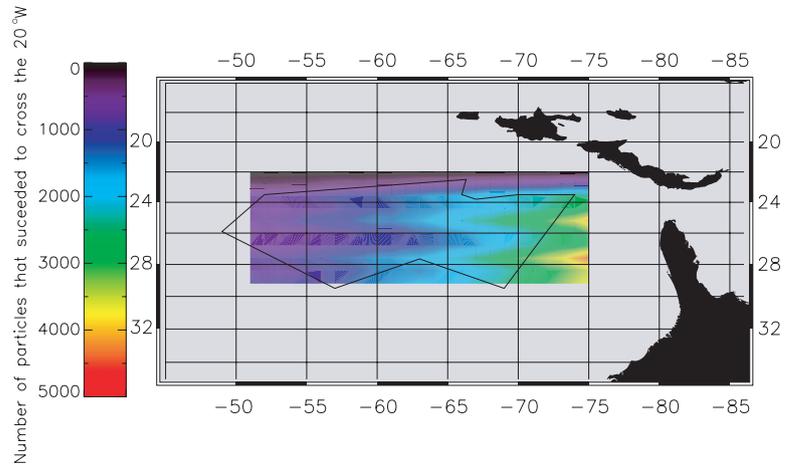
Figure 2. Latitude distribution of particles successfully crossing the 20°W meridian. Particles drift over 1.5 yr after being released within the eel-spawning area for the Drakkar (a) and Mercator (b) models. The maps on the right hand side were drawn up until 20°W, where particles were counted. They show the location of the latitude bins defining the histogram.



70 m depth for the Mercator model. The same patterns of departure and arrival areas were observed for the three experiments, i.e., fixed-depth, vertical migration or fastest current choice. These general

patterns correspond to the results of Kettle and Haines (2006) and confirm the robustness of the results, as the ocean models used do not have the same features as those used by Kettle and Haines (2006).

Figure 3. Number of successful particles as a function of starting location in the Sargasso Sea when using the Drakkar model (colour scale). The European eel-spawning area is charted by a black polygon.



The results of the following sections have been summarized in Tables 1 and 2.

Factors influencing the migration success

Large-scale oceanic indices. Over the whole simulation period, 0.0025 and 0.039% of those particles with a fixed-depth drift, succeeded in crossing the 20°W meridian in less than 1.5 yr (Drakkar and Mercator model, respectively). For both models, we found a significant positive relationship between winter NAO and the number of particles that succeeded in arriving each year (Pearson's $r = 0.50$ and 0.78 , $P = 0.05$ and 0.04 , for Drakkar and Mercator,

respectively; autocorrelation removed following Pyper and Peterman, 1998). The same applies to the GSI ($r = 0.73$ and 0.80 , $P = 0.01$ and 0.04 for Drakkar and Mercator, respectively) and for the PEA ($r = 0.57$ and 0.47 , $P = 0.05$ and 0.06 for Drakkar and Mercator, respectively).

Influence of larvae behaviour. For both models, the two active behaviours of particles tend to diminish the migration success. Over the simulation period, 0.0011 and 0.0004% of those particles, having a vertical diurnal migration, succeeded in crossing 20°W in less than 1.5 yr (Drakkar and Mercator model, respectively). When particles selected the fastest

Figure 4. Depth distributions of the particles successfully crossing the 20°W meridian within 1.5 yr after being released within the eel-spawning area and drifting at fixed-depth for the Drakkar (a) and Mercator (b) models.

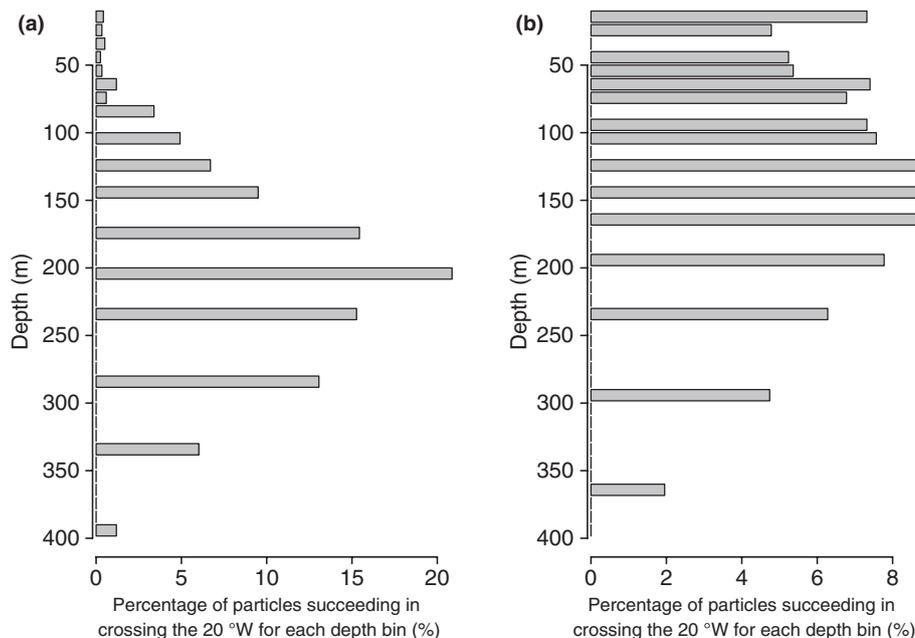


Table 1. Number of particles released that succeeded in crossing the 20°W line, minimum migration duration and distance covered for the fastest particles for the two ocean configurations (Drakkar and Mercator) and the three behaviours (fixed-depth, vertical diurnal migration and fastest current choice).

Ocean configuration	Behaviour	No. of particles released over the whole period	No. of particles succeeding in crossing 20°W (as % of those released)	Minimum migration duration	Distance covered (km)
Drakkar	Fixed-depth	47 342 592	0.0025	10 months 19 days	8447
	Vertical migration	1 972 608	0.0011	1 yr 3 months 1 day	9699
	Fastest current choice	1 972 608	0.0014	1 yr 28 days	9199
Mercator	Fixed-depth	7 602 144	0.039	10 months 3 days	8498
	Vertical migration	475 200	0.0004	1 yr 2 months 18 days	8928
	Fastest current choice	475 200	0.0006	1 yr 2 months 21 days	9748

Table 2. Summary of relationships between the three large-scale oceanic indices [North Atlantic Oscillation (NAO; Hurrell, 1995), Gulf Stream Index (GSI; Taylor and Stephens, 1998), Potential Energy Anomaly (PEA; Curry and McCartney, 2001)] and the arrival success and the minimum migration duration for each simulated year with the Drakkar and Mercator configurations (using the fixed-depth experiment). *r* is Pearson's correlation coefficient and *P*, the significance level (n.s., for non-significant).

Ocean configuration	Lagrangian output tested	NAO		GSI		PEA	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Drakkar	Minimum duration	-0.57	0.04	-0.75	0.01	-0.48	0.05
	Arrival success	0.5	0.05	0.73	0.01	0.57	0.05
Mercator	Minimum duration	-0.40	n.s.	-0.54	0.07	-0.32	n.s.
	Arrival success	0.78	0.04	0.80	0.04	0.47	n.s.

current, the arrival success was still lower than the fixed-depth experiment and similar to the vertical migration hypothesis, i.e., 0.0014 and 0.0006% for the Drakkar and Mercator model, respectively.

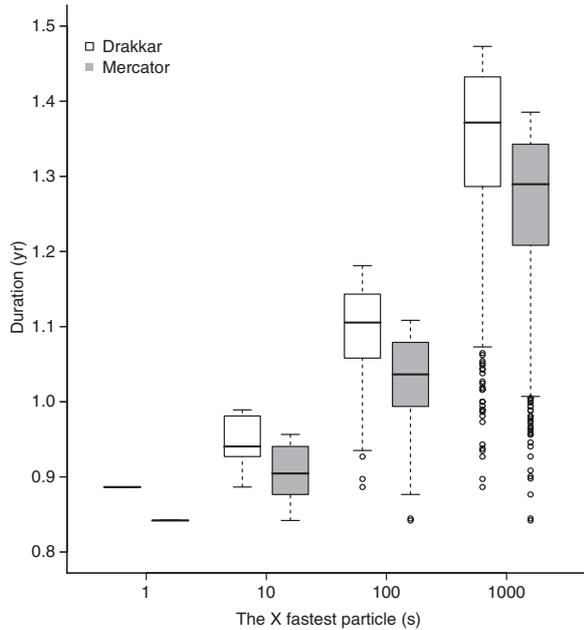
Estimates of migration duration and its determining factors

In the Drakkar model, the fastest particle travelled, at a fixed depth, from the Sargasso Sea (initial position 27.5°N, 74.5°W) to the 'finishing' line in 10 months and 19 days, covering 8447 km. Figure 5 indicates that the migration durations of the 10, 100 and 1000 next particles were much greater than the fastest one. In the Mercator model, the migration duration and the distance covered are very similar to the Drakkar model. The fastest particle travelled at a fixed depth in

10 months and 3 days, and covered 8498 km (initial position 29.73°N, 74.66°W). The duration of the 10, 100 and 1000 fastest particles represented in Fig. 5 confirmed results found with the Drakkar model; the fastest particle was significantly so. The migration routes of the ten fastest particles were similar for both models and were relatively direct (Fig. 6).

Large-scale oceanic indices influence minimum migration duration. Analysis of the relationships between NAO, GSI and PEA, and the minimum migration duration of particles drifting at fixed-depth revealed a negative link between NAO and minimum migration duration ($r = -0.57$, $P = 0.04$ with autocorrelation removal). The same was the case for GSI ($r = -0.75$, $P = 0.01$) and PEA ($r = -0.48$,

Figure 5. Boxplot of migration duration of the fastest particle, the 10 fastest particles, the 100 fastest particles, and the 1000 fastest particles for the Drakkar model (white) and Mercator model (grey). Circles represent individuals outside the confidence interval.

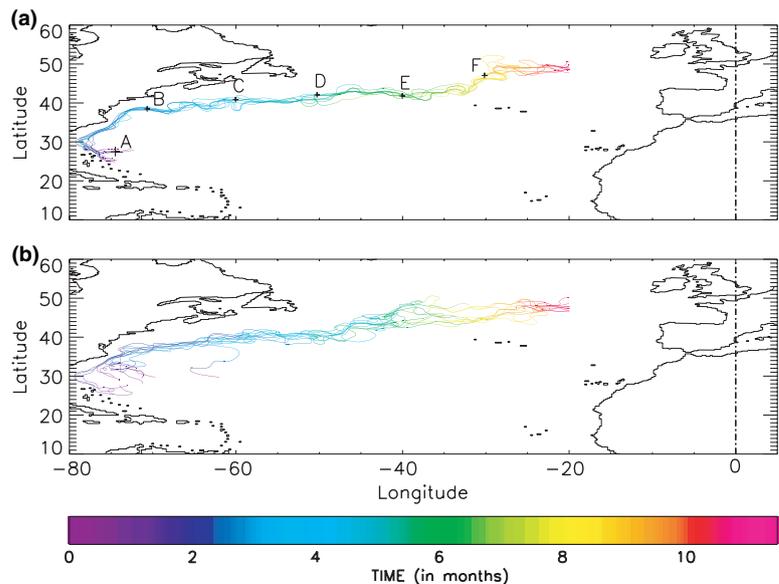


$P = 0.05$). The minimum migration duration occurred for particles starting in 1990 (NAO over the drift equals 2.5 and high GSI and PEA). This indicated that when large-scale indices were high (prevailing westerly winds and high ‘strength’ of the Gulf Stream) the minimum migration duration was shorter. We can assume that the same applies to the migration duration

overall. These results are therefore consistent with the positive correlation found between larval arrival success and large-scale oceanic indices. The faster the migration, the higher the arrival success.

Active behaviour slows down the migration and increases the distance. For both models, when implementing vertical diurnal migration behaviour, the fastest particle took more than 5 months longer compared to fixed-depth experiments, and the distance covered was more than 3000 km longer. With a vertical diurnal migration, the fastest particle travelled from the Sargasso Sea to the ‘finishing’ line in 1 yr, 3 months and 1 day, covering 9699 km, in the Drakkar model, and 1 yr, 2 months and 18 days, covering 8928 km, in the Mercator model. This is the only particle that succeeded in reaching 20°W, and it reached this latitude at a longitude too far south to account for it in our study (5.8°N, off the coast of Liberia), as no eels have been reported there (Schmidt, 1909a). The duration and distance obtained in the second active behaviour (i.e., particles actively shifting from depth layers to select the fastest current velocity) were very similar to the ones obtained in the vertical migration experiment. The fastest particle travelled from the Sargasso Sea to the finishing line in 1 yr and 28 days and covered 9199 km (Drakkar model). When using the Mercator model, three particles succeeded in reaching 20°W. The fastest particle travelled 9748 km in 1 yr, 2 months and 21 days. We did not take into account the other two trajectories as they arrived too far south to be realistic (north of Senegal and south of Mauritania).

Figure 6. Trajectories of the 10 fastest particles that succeeded in crossing the 20°W meridian using the Drakkar model (a) and Mercator model (b). The letters (A–F) represent the positions used to calculate the diagram of zonal velocity at different depths (used in Fig. 7).



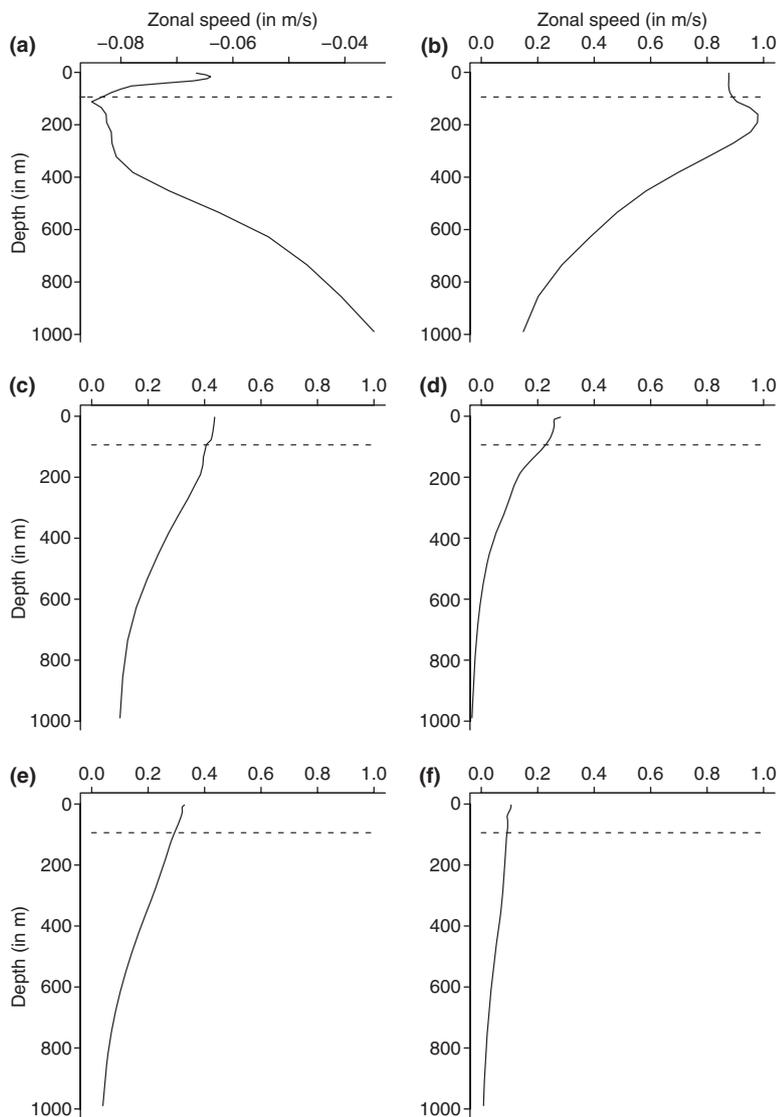


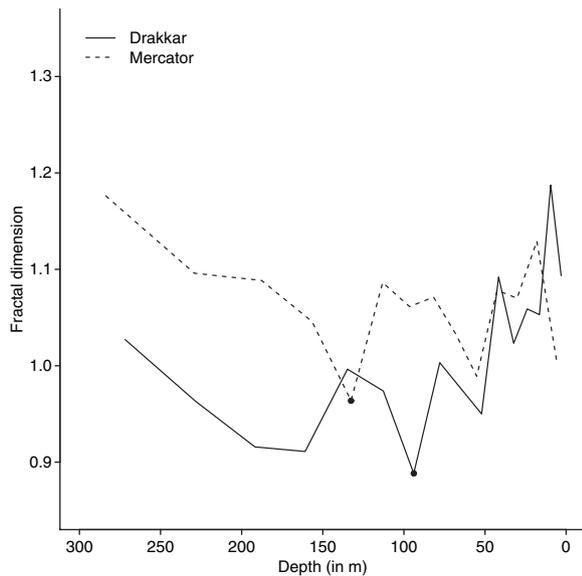
Figure 7. Diagrams of the zonal speed u (West–East) at different depths at positions (described in Fig. 6) of the fastest particle using the Drakkar model. The horizontal dashed line represents the depth of the fastest particle (94 m) found when running on the Drakkar model.

To understand possible sources that could lead to such discrepancies between fixed-depth and active behaviour experiments, we analysed the trajectories and physical conditions that particles encounter along their drift. Figure 7 shows transects of zonal velocity (East–West) carried out at different trajectory locations of the fastest particle in the Drakkar model (Fig. 6). Figure 7 shows that the zonal speed is negative (i.e., from East to West) when particles leave the Sargasso Sea, and positive thereafter. The velocity transects highlight the fact that the layer where the fastest particle drifted (–94 m) was most of the time the layer with the fastest velocity.

Fractal dimension analysis confirmed that migration duration was closely associated with the linearity of the trajectories. The more linear the trajectory (the

lower the fractal dimension D), the shorter the migration duration. For each depth, the fractal dimension of the trajectories of the fastest particle is represented in Fig. 8. The fractal dimension was the lowest for the depth –94 m ($D = 0.88$; Drakkar model) and –132 m ($D = 0.96$; Mercator model) (solid circles in Fig. 8). These depths correspond to the depths where the particles had the fastest migration duration as well. This confirms that the fastest particles have less wiggly trajectories. For these depths, the fractal dimension was close to one. In fractal theory, a continuous line (i.e., an infinite number of points) typically has the value of unity. Here, the trajectory was close to a line but has a finite number of points. Hence the fractal dimension was just below one.

Figure 8. Fractal dimensions of the trajectory of the fastest particle in each depth of the Drakkar model (solid line) and the Mercator model (dashed line). The solid circle represents the depth of drift of the fastest particle in each model.



DISCUSSION

Simulations fit with observations

The general results regarding departure, arrival areas and the depth of drift are consistent with observations of leptocephali for both models. Most particles that succeeded in crossing the Atlantic in less than 1.5 yr came from the Western Sargasso Sea. This is mainly due to the proximity to the Gulf Stream. Particles nearby can enter the Gulf Stream in less time than those more easterly spawned particles that drift in the slow currents of the Sargasso Sea (Kleckner and McCleave, 1982; see Fig. 7, panel A). The smallest larvae found in that area were also located in the western part of the Sargasso Sea (see Fig. 2 in McCleave *et al.*, 1987). The distribution area of particle arrivals fits well with the distribution area of the European eel (e.g., Schmidt, 1909a). This distribution is, however, mainly centred on West Europe at 20°W, with another peak in North Africa for the Mercator model, as found by Kettle and Haines (2006). In the Drakkar model, the Azores Current is weakly represented, which explains why the lowest proportion of particles arrived at Morocco. Regarding the fixed-depth experiment, the depth range (–50 to –400 m) of particles crossing 20°W in less than 1.5 yr corresponds to the observed depths of leptocephali (e.g., Castonguay and McCleave, 1987) and to the study carried out by Kettle and Haines (2006).

The positive relationships between oceanic indices such as the NAO, GSI (latitude of the Gulf Stream) and PEA (strength of the Gulf Stream), and the number of successful particles per year are consistent. This indicates that a larger number of particles reached 20°W when transport conditions were favourable (Kettle *et al.*, 2008). These results are consistent with the negative link between oceanic indices and the minimum migration duration.

A minimum limit of the migration duration

Potential influence of natural mortality. The aim of this study was not to estimate the mean migration duration of eel larvae but to investigate the minimum migration duration of a passive drifter from the Sargasso Sea to the European shelves. The estimation of the real mean migration duration using a Lagrangian model would require mortality to be taken into account. Indeed, the histogram of the migration duration of particles cannot be used to estimate the mean migration duration because accounting for mortality, which is thought to be roughly exponential with time, will drastically change the distribution of migration duration (Cowen *et al.*, 2000; Hare *et al.*, 2002). Particles with a long migration duration, experience high mortality relative to particles with shorter migration duration. As eel larval mortality is still unknown, we preferred not to undertake such an analysis and focussed instead on the fastest particles. But it is noteworthy that accounting for mortality during the migration duration will necessarily lead to an equal or greater minimum bound for migration duration.

Drifting at fixed depth is the fastest way. The fastest particle was observed when drifting at fixed depths for both models (–94 m for Drakkar and –132 m for Mercator), crossing the Atlantic Ocean in more than 10 months. The two conditions required for the fastest migration are that particles spend most of their time in the fastest layer and that the fractal dimensions of their trajectories are the lowest. The hypothesis of an active vertical diurnal migration is the most realistic in terms of eel ecology. Although less realistic, the behaviour consisting in actively selecting the depth layer with the highest current velocity at each time step was a valuable scenario to be tested, as it increased the range of possible trajectories investigated. However, both these active behaviours lead to far longer migration duration and distance. In particular, the vertical migration in upper layers (higher fractal dimension) made the particles drift in eddies and hence increased the migration duration. Consequently, the diel migration behaviour of leptocephali is certainly not a

way to maximize the use of the current velocity. As leptocephali are planktonic feeders, the vertical migration would surely be driven by feeding needs and, overall, corresponds to the observed diurnal migration of plankton (e.g., Steinberg *et al.*, 2002). It could be a way to avoid predators as well.

Interestingly enough, active behaviours led particles to reach the West Africa coast, where no eels have hitherto been found except in Morocco. As the aim of this study was to find the shortest migration duration to reach European shelves, we could not explain these 'misfit' particles. However, it is interesting that this pathway is possible and that eel larvae can reach the West African shelf with a reasonable migration duration. This result fits with Kettle and Haines (2006), who found the same 'hypothetic' pathways.

Potential sources of underestimation of the passive drift speed. Most successful particles started west of the release area (Fig. 3). This corresponded with the fastest particles, but probably does not represent the area where most spawning occurs. This might be located in more easterly areas. Drifting times, from the eastern spawning area to the Gulf Stream, were therefore neglected, although this is known to be a region with slow currents (McCleave and Kleckner, 1987).

We chose an arbitrary 'finishing' line still at a distance from the European shelf (1000 km from Ireland and 1500 km from France). This distance needs to be covered in addition to metamorphosis, which is estimated to occur over 18–52 days (Arai *et al.*, 2000), 33–76 days (Lecomte-Finiger, 1992) or 98 days (Wang and Tzeng, 2000). By removing these three steps, we have underestimated the migration duration. The migration duration from Lagrangian simulations corresponded to the estimated age of leptocephali before their metamorphosis on the continental slope (Schmidt, 1909b; McCleave, 1987; Antunes and Tesch, 1997). The finishing line was located before the continental slope. The drift duration to reach 20°W is surely shorter than the age before metamorphosis estimated by otolith microstructure, as a long distance remains to be covered until the continental slope is reached.

We used off-line computations, whereas ideally we would use on-line computations, for estimating the computed velocity at each model time step to integrate trajectories. Working with averaged quantities (the archived fields of a simulation) can introduce biases in trajectory calculations. As opposed to that, off-line calculations, such as those used in this study, offer much more flexibility and discernment in the definition of the Lagrangian experiments, without the

cost of re-running a full ocean model. Our study dealt with models with horizontal grids between eddy-permitting and fully eddy-resolving resolution. Furthermore, the Drakkar model uses air–sea fluxes that rely on the <1° (at the equator) ERA-40 6-h atmospheric re-analysis. The Mercator simulation makes use of equivalent re-analyses of surface atmospheric variables, but was run at 1/3° resolution, which puts it more on the eddy-permitting side. As a matter of fact, for both models, the intrinsic scales of variability were long enough to be fairly well sampled with a 5-day archiving strategy for the Drakkar model, and appropriately sampled with a 1-day archiving strategy for the Mercator model. In other respects, one must not forget that the Drakkar simulation has the unique advantage of being long enough to address interannual (or even interdecadal) variability, though of course to the detriment of the sharpness of the time sampling of its archive. As already shown by McClean *et al.* (2002), a change in model resolution goes with significant change in the characteristic length scales associated with the movement of numerical drifters: Lagrangian integral time scales of the order of a few days, typical of genuinely observed drifter displacements in the North Atlantic, can only be recovered with high-resolution modelling, whereas coarser models tend to overestimate such quantities (just as the two simulations we used). Such conclusions lend confidence to our analysis run using 5-day model outputs for the Drakkar simulation and encourage us to favour a more frequent (daily) storage when dealing with much finer horizontal resolution.

Indeed, using ocean general circulation models that do not fully resolve mesoscale eddies, we underestimated the distance covered by particles and/or overestimated the drift speed. The Drakkar and Mercator models are among the most precise models currently running for model ocean circulation, with resolutions of 1/4° and 1/3°, respectively. It would be interesting to assess the impact of the use of higher resolution models on the speed and the distance covered by particles. When using Drakkar (the best resolution of the two models), the migration duration is slightly longer than with Mercator. This phenomenon is highlighted in Fig. 5. The use of higher resolution models (for instance 1/12°) would have enabled us to determine mesoscale eddies more accurately (Smith *et al.*, 2000). When improving the resolution of a ocean general circulation model, two combined effects could be observed: the maximal speed was higher but particles had longer trajectories, as they could be trapped in mesoscale eddies. Further studies could analyse possible

consequences of the use of a higher resolution model on the migration duration.

Do leptocephali swim to reach European shelves?

Our results clearly contrast with the analysis of otolith microstructure (e.g., Lecomte-Finiger, 1992). When considering the migration duration inferred from otolith microstructure, eel larvae would be able to reach European coasts in 6 months. In contrast, our estimates of a minimum bound for migration duration were about 10 months.

It should be noted that the results of otolith analyses remain questionable (McCleave, 2008). The reading accuracy of daily growth increments has sparked a wide debate (e.g., Antunes and Tesch, 1997; McCleave *et al.*, 1998). To our knowledge, the age estimation of eel larvae from daily increments has never been validated for the European eel. Leptocephali may have such a low metabolic rate that increments in otoliths might not be deposited daily, or be deposited daily but be too thin to be observed in scanning electron microscopy. We refer to Bonhommeau *et al.* (in press) for a complete description of possible sources of misinterpretation of otolith microstructure.

It is also interesting to question the implications of such short migration duration (6 months) in terms of swimming speed. Using the drift distance and migration of the fastest particle in the Drakkar model, the mean passive drift speed (Equation 1) is 30.2 cm s^{-1} . The required speed to cover the same distance in 6 months is $8447 \text{ km} / 6 \text{ months} = 54.3 \text{ cm s}^{-1}$, which would be possible with an active swimming speed of $54.3 - 30.2 = 24.1 \text{ cm s}^{-1}$. In the Mercator model, the mean passive drift speed of the fastest particle is 32.0 cm s^{-1} . Using the same calculation, the required speed to cover the 8498 km in 6 months is 54.6 cm s^{-1} , leading to a required active swimming speed of 22.6 cm s^{-1} . Arai *et al.* (2000) estimated that the age at metamorphosis may be higher than those found by Lecomte-Finiger (1992, 1994), which is a mean age of 198 days. In that case, the required speed would be 19.2 and 17.7 cm s^{-1} for the Drakkar and Mercator models, respectively. Our approach then suggests that such a short migration would require an active swimming speed of around $18\text{--}24 \text{ cm s}^{-1}$. This means that leptocephali should swim at least at 3.4 body lengths s^{-1} (body length of a fully-developed leptocephali, which is about 70 mm long; Schmidt, 1922, 1923) for more than 8400 km (the distance travelled by the fastest particle; Fig. 5). Particles that have a longer passive drift will have to have a faster swimming speed. This hypothetical swimming speed assumes a perfect orientation of leptocephali, and this

has not been demonstrated. Also, the ten fastest particles followed direct routes (Fig. 6a,b) and even an active oriented swimming would not have enabled them to reach the European shelf more directly.

The hypothesis of active and oriented swimming, asserted to make possible the 6-month migration duration of eel larvae, appears spurious with regard to the present results. Indeed, although such swimming speeds are observed for migrating adult fish (Blaxter, 1969), the energy expenditure required seems unrealistic for eel larvae, as the open ocean is a low productive area (Raven *et al.*, 2007). Moreover, swimming activity would need developed muscles, but according to McCleave *et al.* (1998): leptocephali [...] have only minute amounts of subcutaneous red muscle (Leonard and Summers, 1976).

CONCLUSION

We investigated the minimum migration duration of passive particles as they drift from the Sargasso Sea to the European shelf. To do this we used high-resolution ocean general circulation models. By contrast to Kettle and Haines (2006), we examined the possible influences of active behaviour of particles (vertical diurnal migration and faster current choice) on migration duration. We show that active behaviours are not a way to minimize the migration duration but, on the contrary, increase the migration duration. Our results show that very few particles reach 20°W in less than 1 yr (one over several millions) and that the crossing in 6 months, thanks to an active and oriented swimming, would require a very fast swimming speed (more than 3.4 body length s^{-1}) over a very long distance (more than 8000 km). Such energy expenditure is not possible in low productive areas such as the open ocean. We did not consider the swimming ability of leptocephali (e.g., Bishop and Torres, 1999); however, this swimming capacity could not be used to reach European shelf significantly faster than with the passive drift.

ACKNOWLEDGEMENTS

We thank Gaëtan Vinay the GIP Mercator Ocean (Toulouse, France) for providing the Mercator circulation fields (PSY1v2) and Jean-Marc Molines (CNRS, LEGI, Grenoble) who provided the Drakkar model simulation. The Drakkar model was run at the IDRIS computing centre of CNRS, Orsay, France. We thank Roger Le Du for the orthodromic distance calculation. We thank James Watson for English improvements and suggestions. We thank James McCleave and Karen

Edwards and one other anonymous referee for their in-depth review and helpful comments.

REFERENCES

- Aguilar, A., Alvarez, M.F., Leiro, J.M. and Sanmartin, M.L. (2005) Parasite populations of the European eel (*Anguilla anguilla* L.) in the Rivers Ulla and Tea (Galicia, northwest Spain). *Aquaculture* **249**:85–94.
- Anonymous (2003). Worldwide decline of eel resources necessitates immediate action – Québec declaration of concern. *Fisheries* **28**:28–30.
- Antunes, C. and Tesch, F.-W. (1997) A critical consideration of the metamorphosis zone when identifying daily rings in otoliths of European eel, *Anguilla anguilla* (L). *Ecol. Freshw. Fish.* **6**:102–107.
- Arai, T., Otake, T. and Tsukamoto, K. (2000) Timing of metamorphosis and larval segregation of the Atlantic eels *Anguilla rostrata* and *A. anguilla*, as revealed by otolith microstructure and microchemistry. *Mar. Biol.* **137**:39–45.
- Barnier, B., Madec, G., Penduff, T. et al. (2006) Impact of partial steps and momentum advection schemes in a global ocean circulation model at eddy permitting resolution. *Ocean Dyn.* **56**:543–567.
- Baugrand, G. and Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Chang. Biol.* **9**:801–817.
- Bertin, L. (1956) *Eels, a Biological Study*. London: Cleaver-Hume Press Ltd.
- Bishop, R.E. and Torres, J.J. (1999) Leptocephalus energetics: metabolism and excretion. *J. Exp. Biol.* **202**:2485–2493.
- Blanke, B. and Raynaud, S. (1997) Kinematics of the Pacific Equatorial Undercurrent: a Eulerian and Lagrangian approach from GCM results. *J. Phys. Oceanogr.* **27**:1038–1053.
- Blanke, B., Arhan, M., Madec, G. and Roche, S. (1999) Warm water paths in the equatorial Atlantic as diagnosed with a general circulation model. *J. Phys. Oceanogr.* **27**:1038–1053.
- Blanke, B., Speich, S., Madec, G. and Döös, K. (2001) A global diagnostic of interocean mass transfers. *J. Phys. Oceanogr.* **31**:1623–1632.
- Blaxter, J.H.S. (1969) Swimming speed of fish. *Tech. Rep. Fish. Rep.* **62**:69–100. Rome: FAO.
- Bolliet, V., Lambert, P., Rives, J. and Bardonnet, A. (2007) Rhythmic swimming activity in *Anguilla anguilla* glass eels: synchronisation to water current reversal under laboratory conditions. *J. Exp. Mar. Biol. Ecol.* **344**:54–66.
- Bonhommeau, S., Chassot, E. and Rivot, E. (2008) Fluctuation in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso Sea. *Fish. Oceanogr.* **17**:32–44.
- Bonhommeau, S., Castonguay, M., Rivot, E., Sabatié, R. and Le Pape, O. (in press) The oceanic life and migration duration of American and European eel larvae. *Fish Fish.*
- Castonguay, M. and McCleave, J.D. (1987) Vertical distributions, diel and ontogenic vertical migrations and net avoidance of leptocephali of *Anguilla* and other common species in the Sargasso Sea. *J. Plankton Res.* **9**:195–214.
- CITES (2007) Additional information concerning proposal cop14 prop. 18 on the European eel (*Anguilla anguilla*). vol. CoP14 Inf. 21. Convention on International Trade in Endangered Species of Wild Fauna and Flora (<http://www.cites.org/common/cop/14/inf/E14i-21.pdf>).
- Cowen, R.K., Iwiza, K.M.M., Sponaugle, S., Paris, C.B. and Olson, D.B. (2000) Connectivity of marine populations: open or closed? *Science* **287**:857–859.
- Curry, R.G. and McCartney, M.S. (2001) Ocean gyre circulation changes associated with the North Atlantic Oscillation. *J. Phys. Oceanogr.* **31**:3374–3400.
- Dekker, W. (1998) Long-term trends in the glasseels immigrating at Den Oever, the Netherlands. *Bull. Fr. Peche Piscic.* **349**:199–214.
- Dekker, W. (2004) What caused the decline of the Lake IJsselmeer eel stock after 1960? *ICES J. Mar. Sci.* **61**:394–404.
- Feunteun, E. (2002) Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. *Ecol. Eng.* **18**:575–591.
- Friedland, K.D., Miller, M.J. and Knights, B. (2007) Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. *ICES J. Mar. Sci.* **64**:519–530.
- van Ginneken, V., Ballieux, B., Willemze, R. et al. (2005) Hematology patterns of migrating European eels and the role of EVEX virus. *Comp. Biochem. Physiol. C* **140**:97–102.
- Greiner, E., Benkiran, M., Blayo, E. and Dibarboue, G. (2006). *MERA-11 General Scientific Paper, 1992–2002 PSYIV2 Reanalysis*. Tech. rept. reference MOO-MR-431-37-MER. Mercator-Ocean, 8-10 rue Hermès, 31520 Ramonville St. Agne, France.
- Hare, J.A., Churchill, J.H., Cowen, R.K., Berger, T.J., Cornillon, P.C., Dragos, P., Glenn, S.M., Govoni, J.J. and Lee, T.N. (2002) Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. *Limnol. Oceanogr.* **47**:1774–1789.
- Hjort, J. (1914) Fluctuations in the great fisheries of Northern Europe. *Rap. Proces. ver. Con. Int. Exp. Mer* **20**:1–228.
- Hurrell, J.W. (1995) Decadal trends in the North-Atlantic Oscillation – Regional temperatures and precipitation. *Science* **269**:676–679.
- Jørgensen, P.E.V., Castric, J., Hill, B., Ljungberg, O. and Dekinkelin, P. (1994) The occurrence of virus-infections in elvers and eels (*Anguilla anguilla*) in Europe with particular reference to VHSV and IHNV. *Aquaculture* **123**:11–19.
- Kettle, A.J. and Haines, K. (2006) How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean? *Can. J. Fish. Aquat. Sci.* **63**:90–106.
- Kettle, A.J., Bakker, D.C.E. and Haines, K. (2008). Impact of the North Atlantic Oscillation on the trans-Atlantic migrations of the European eel (*Anguilla anguilla*). *J. Geophys. Res. Ocean* **113**, GE03004, doi:10.1029/2007JG000589.
- Kleckner, R.C. and McCleave, J.D. (1982) Entry of migrating American eel leptocephali into the Gulf Stream system. *Helgoland Mar. Res.* **35**:329–339.
- Knights, B. (2003) A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. *Sci. Total Environ.* **310**:237–244.
- Kuroki, M., Momoko, K., Jónsson, B. et al. (2008) Inshore migration and otolith microstructure/microchemistry of anguillid glass eels recruited to Iceland. *Environ. Biol. Fish* **83**:309–325.
- Lecomte-Finiger, R. (1992) Growth history and age at recruitment of European glass eels (*Anguilla anguilla*) as revealed by otolith microstructure. *Mar. Biol.* **114**:205–210.

- Lecomte-Finiger, R. (1994) The early-life of the European Eel. *Nature* **370**:424.
- Lehodey, P., Alheit, J., Barange, M. *et al.* (2006) Climate variability, fish, and fisheries. *J. Clim.* **19**:5009–5030.
- Leonard, J.B. and Summers, R.G. (1976) The ultrastructure of the integument of the American eel, *Anguilla rostrata*. *Cell Tissue Res.* **171**:1–30.
- Madec, G. (2008) NEMO ocean engine. *Note du pôle de modélisation* **27**. Paris: Institut Pierre-Simon Laplace (IPSL).
- McClellan, J., Poulain, P. and Pelton, J.W. (2002) Eulerian and Lagrangian statistics from surface drifters and a high-resolution POP simulation in the North Atlantic. *J. Phys. Oceanogr.* **32**:2472–2491.
- McCleave, J.D. (1987). Migration of *Anguilla* in the ocean signposts for adults! Signposts for leptocephali? In: *Signposts in the Sea: Proceedings of a Multidisciplinary Workshop on Marine Animal Orientation and Migration*. 29–31 May 1986. W.F. Herrnkind & A.B. Thistle (eds) Tallahassee, FL, USA: Florida State University Conference Center. pp. 102–117.
- McCleave, J.D. (1993) Physical and behavioral controls on the oceanic distribution and migration of leptocephali. *J. Fish Biol.* **43**:243–273.
- McCleave, J.D. (2001) Simulation of the impact of dams and fishing weirs on reproductive potential of silver-phase American eels in the Kennebec River basin, Maine. *North Am. J. Fish. Manage.* **21**:592–605.
- McCleave, J.D. (2008) Contrasts between spawning times of *Anguilla* species estimated from larval sampling at sea and from otolith analysis of recruiting glass eels. *Mar. Biol.* **155**:249–262.
- McCleave, J.D. and Kleckner, R.C. (1987) Distribution of leptocephali of the catadromous *Anguilla* species in the Western Sargasso Sea in relation to water circulation and migration. *Bull. Mar. Sci.* **41**:789–806.
- McCleave, J.D., Kleckner, R.C. and Castonguay, M. (1987) Reproductive sympatry of American and European eels and implications for migration and taxonomy. *Am. Fish. Soc. Symp.* **1**:286–297.
- McCleave, J.D., Brickley, P.J., O'Brien, K.M. *et al.* (1998) Do leptocephali of the European eel swim to reach continental waters? Status of the question *J. Mar. Biol. Assoc. UK* **78**:285–306.
- Palstra, A.P., van Ginneken, V.J.T., Murk, A.J. and van den Thillart, G.E.E.J.M. (2006) Are dioxin-like contaminants responsible for the eel (*Anguilla anguilla*) drama? *Naturwissenschaften* **93**:145–148.
- de Pison, F.J.M., Mere, J.O., Limas, M.C. and de Cos Juez, F.J. 2007 *fdim: Functions for Calculating Fractal Dimension*. R package version 1.0-5. Vienna, Austria: R Foundation for Statistical Computing.
- Pyper, B.J. and Peterman, R.M. (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**:2127–2140.
- R Development Core Team. (2007). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raven, P.H., Johnson, G.B. and Losos, J.B. (2007). *Biologie*, 7th edn, Paris, France: De Boeck.
- Schmidt, J. (1909a). On the distribution of the fresh-water eels (*Anguilla*) throughout the world. I. Atlantic Ocean and adjacent regions. *Meddelelser fra Kommissionen for Havundersøgelser, Seri Fiskeri III*:1–45.
- Schmidt, J. (1909b). Remarks on the metamorphosis and distribution of the larvae of the eel (*Anguilla vulgaris* Turt.). *Meddelelser fra Kommissionen for Havundersøgelser, Seri Fiskeri III*:1–17.
- Schmidt, J. (1922) The breeding places of the eels. *Philos. Trans. R. Soc. B Biol. Sci.* **211**:179–208.
- Schmidt, J. (1923) Breeding places and migrations of the Eel. *Nature* **111**:51–54.
- Schoth, M. and Tesch, F.-W. (1984) The vertical-distribution of small 0-group *Anguilla* larvae in the Sargasso Sea with reference to other Anguilliform leptocephali. *Meeresforschung* **30**:188–195.
- Smith, R.D., Maltrud, M.E., Bryan, F.O. and Hecht, M.W. (2000) Numerical simulation of the North Atlantic Ocean at 1/10 degrees. *J. Phys. Oceanogr.* **30**:1532–1561.
- Steinberg, D.K., Goldthwait, S.A. and Hansell, D.A. (2002) Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep-Sea Res. Part I* **49**:1445–1461.
- Taylor, A.H. and Stephens, J.A. (1998) The North Atlantic oscillation and the latitude of the Gulf Stream. *Tellus Ser. A* **50**:134–142.
- Tréguier, A.-M., Theetten, S., Chassignet, E. *et al.* (2005) The North Atlantic subpolar gyre in four high-resolution models. *J. Phys. Oceanogr.* **35**:757–774.
- Wang, C.H. and Tzeng, W.N. (2000) The timing of metamorphosis and growth rates of American and European eel leptocephali: A mechanism of larval segregative migration. *Fish. Res.* **46**:191–205.