Estimates of the mortality and the duration of the trans-Atlantic migration of European eel Anguilla anguilla leptocephali using a particle tracking model

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Abstract:

Using Lagrangian simulations, based on circulation models over three different hydroclimatic periods in the last 45 years in the North Atlantic Ocean, the trans-Atlantic migration of the European eel Anguilla anguilla leptocephali was simulated via the passive drift of particles released in the spawning area. Three different behaviours were modelled: drifting at fixed depth, undergoing a vertical migration or choosing the fastest currents. Simulations included mortality hypotheses to estimate a realistic mean migration duration and relative survival of A. anguilla larvae. The mean migration duration was estimated as 21 months and the mortality rate as 3·8 per year, i.e. < 0·2% of A. anguilla larvae may typically survive the trans-Atlantic migration.

Keywords: Lagrangian modelling • leptocephalus mortality • migration duration

INTRODUCTION

The European eel (*Anguilla anguilla* L.) is a catadromous fish that goes through a long oceanic spawning migration, from continental growth habitats more than 6,000 km across the Atlantic Ocean to the Sargasso Sea. Eel larvae (leptocephali) then return, metamorphosing as they reach the continental shelf into glass eels that settle in European and North African freshwaters, estuaries and coastal waters, from Mauritania to the Polar Circle (Schmidt, 1923; Tesch, 2003).

The oceanic larval phase of European eels is of great importance in understanding eel population dynamics. As for many marine fish species, the major source of mortality occurs during the larval stage (Hjort, 1914). The oceanic phase determines the dispersion over the coastal regions and the freshwater habitats (Kettle & Haines, 2006). The migration duration is certainly one of the most critical and controversial features of the oceanic biology of eel larvae. It is related to eel larval oceanic trajectories and mortality, and hence it determines dates and areas of arrival at the coast. It also determines our ability to understand how recruitment is linked to environmental fluctuations. This is critical in a context where major changes in oceanic conditions are recorded and known to impact fish populations (Beaugrand & Reid, 2003; Lehodey *et al*., 2006). 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*., 2008a). Fluctuations in sea temperature and primary production in the spawning area have been shown to be related to glass eel recruitment (Knights, 2003; Bonhommeau *et al*., 2008). However, all these studies used recruitment indices based on glass eel arrivals. Because oceanic environmental conditions must affect leptocephali several months earlier than glass eel arrivals, time lags have to account for migration duration to link environmental descriptors to glass eel recruitment. Results still

45 remain conditioned by the assumption made about migration duration, e.g. 1-year lag for

Friedland *et al*. (2007), environmental conditions integrated over 2.5 - 3 years for Knights

(2003) and a 2.5 -3 year lag for Bonhommeau *et al*. (2008).

These hypotheses rely on different estimates depending upon the methods used. While

cohort analyses (Schmidt, 1922), otolith macrostructure analyses (van Utrecht and Hollebom

50 (1985) and particle-tracking models (Kettle & Haines, 2006) show a long migration duration

(more than two years), the analyses of the otolith microstructure estimate that the migration

duration is shorter than 1 year (Lecomte-Finiger, 1992; Wang & Tzeng, 2000). The

hypotheses proposed to explain a short migration duration is a hypothetical active and

oriented swimming of eel leptocephali (see Bonhommeau *et al.*, accepted, for further

55 descriptions). Improving our knowledge of the oceanic migration duration is a prerequisite to

a better understanding of the effects of the oceanic environment on eel larvae and subsequent

recruitment.

Recently, it has been shown how general circulation models may provide insights to

better understand larval trans-oceanic migration. Kettle & Haines (2006) used Lagrangian

60 simulations over a 4-year period (1993-1996) to estimate the migration duration and pathways

of European eel larvae and found a 2-year duration to 25°W. However, Kettle & Haines

(2006) used fixed-depth passively-drifting particles to analyse migration routes and duration.

This assumption remains questionable as leptocephali show vertical diurnal migrations (e.g.

Castonguay & McCleave, 1987) and might be able to select faster current velocities at

65 different depths. Here the hypothesis of strict passive and fixed-depth drift of particles is

relaxed. To do so, other particle trajectories are explored using two other behaviours

(although biologically unrealistic) that enable assessment of their impact on migration

duration and mortality. These issues are addressed in the present study by comparing results

from three different behaviours of the particles: (*i*) particles drifting at fixed-depth as in Kettle & Haines (2006), (*ii*) particles undergoing a vertical diurnal migration between 300m and 50m as observed in the wild (Castonguay & McCleave, 1987), (*iii*) particles drifting at the depth where the velocity of currents (whatever the direction) is the highest. Moreover, Kettle & Haines (2006) recognized that their approach suffered from a critical drawback in that it did not account for mortality of particles during migration; with no mortality, even the slowest particles will succeed in reaching the 'finishing' line and the mean duration will be pushed toward unrealistic high values. Conversely, if mortality is included, the slowest particles have a greater chance of dying than the fastest ones and a strong negative correlation would be expected between mean migration duration and mortality.

In this paper, this issue is addressed by combining the results of Lagrangian simulations with current knowledge gathered from the literature which allows estimation of the mortality of leptocephali. The different mortality estimates over the whole life cycle, except the leptocephalus stage, enabled estimation of the mortality of eel leptocephali under a steady-state hypothesis of eel population, *i.e.* no increase nor decrease of the population size. The range of credible values for the mortality during the oceanic larvae stage is hence restricted. This, in turn, allows for drastic restrictions of the range of estimated migration duration from Lagrangian simulations, helping to provide a more realistic estimate of the mean migration duration.

MATERIALS AND METHODS

CIRCULATION MODELS

Lagrangian simulations were performed using an ocean general circulation configuration, the Drakkar model, that is currently one of the most accurate in the European

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scientific community involved in realistic basin-scale ocean modelling. Simulations were possible over a period of 45 years. The Drakkar model (http://www.ifremer.fr/lpo/drakkar) is based on the NEMO/OPA numerical code (Madec *et al*., 1998) and is useful because of the duration of the simulation (1958 to 2004), which allows it to address the interannual variability of trajectories over decadal time scales. The model configuration is global. The model configuration is global, using the ORCA025 grid (a tripolar grid with a 1/4° horizontal resolution at the equator). Barnier *et al*. (2006) described this configuration and showed its good performance in representing strong currents and eddy variability, even in comparison 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 state of the art atmospheric data (a blend of satellite products and ERA40 6-hourly winds, temperature and humidity). The Drakkar model is a so-called 'fully prognostic' model, which means that it does not use assimilated ocean data (satellite altimetry, *in-situ* temperature or salinity) and therefore can be substantially different from observations in some areas, e.g. subpolar regions (Tréguier *et al*., 2005). Fortunately those biases are less pronounced in the subtropical gyre, including the Sargasso Sea. To reduce file size and to centre on the North Atlantic Ocean, simulations were restricted to a subregion ranging from 82 to 6°W and 10 to 60°N. Since the observed depth selected by leptocephali ranges between 50 and 300 m (e.g. Castonguay & McCleave, 1987), the oceanic model was limited to the top 24 levels (3 to 989 m). To avoid the early spin-up phase of the model, the study was restricted to the period 1960-2004 of the simulation. Circulation fields were time-mean archived every 5 days.

LAGRANGIAN SIMULATION DESIGNS

The Ariane tool was used, as developed by B. Blanke and N. Grima, Laboratoire de

115   Physique des Océans, CNRS-IFREMER-IRD-UBO, Brest, France (http://www.univ-

brest.fr/lpo/ariane). It is a FORTRAN code 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 NEMO/OPA to compute analytically trajectories

120   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 & Raynaud,

1997; Blanke *et al*., 1999; Blanke *et al*., 2001). For each simulation year, passive drifters were

released in each model grid cell, i.e. every 1/4 degree and in each vertical level in an area

125   enclosing the assumed spawning area of eels in the Sargasso Sea (Fig. 1 and Fig. 2 in

McCleave & Kleckner, 1987). Particles were released every 15 days throughout the year.

Although spawning occurs during late winter and spring (e.g. McCleave *et al*., 1987),

particles were released throughout the year to explore a wider range of possible trajectories.

This enabled investigation of possible seasonal variations in migration duration. A total of

130   1,972,608 particles were released each year. Particles were allowed to drift over a 5-year

period, which is long enough to encompass the probable maximum migration duration of

European eel larvae, according to the different estimates discussed earlier.

[Figure 1 about here.]

Output files of Lagrangian simulations included position (longitude, latitude, depth)

135   and time for each particle. Particles were considered as having 'succeeded' in their migration

when crossing longitude 20°W, whatever the latitude (see Fig.1). This finish line is more

eastward than the 25°W limit chosen by Kettle & Haines (2006). Since the aim of the study was to estimate the mean migration duration, the finish line has to be as close as possible to the actual arrival area of eel leptocephali to compare to current estimates based on glass eel

140   recruitment to continental habitats. However, 20°W is a reasonable limit since longitudes to the east correspond to the continental slope which is not as well-resolved by the physical model as the open ocean. Moreover, the design of the Lagrangian simulations was unable to represent selective tidal-stream transport or active swimming of glass eels when they reach the shelves (e.g. Gascuel, 1986).

145   The North Atlantic Oscillation index (NAO-index; Hurrell, 1995) is a large scale and integrative index that is derived from the difference between sea level pressure in Lisbon, Portugal and Reykjavick, Iceland. It is correlated with oceanic transport via the strength (Transport index, Curry & McCartney, 2001) and latitude (Gulf Stream index, Taylor & Stephens, 1998) of the Gulf Stream. For comparative purposes, three periods of low, average

150   and high NAO were selected for simulations, i.e. 1960-1964 (mean NAO index= -1.7), 1973-1977 (0.9), and 1986-1993 (3.2). Thus 18 years of particle releases were simulated in total, with the longest period (8 years) encompassing the period of increasing NAO index but also the decline in eel recruitment (Bonhommeau *et al*., 2008).

          The behaviour of leptocephali during their transatlantic migration may impact on their

155   migration duration and mortality. Therefore, three particle behaviours were implemented in Lagrangian simulations. The first assumed a fixed depth drift for all particles released at each vertical level of the reduced model. It is not grounded on biological observations but enabled comparison with Kettle & Haines (2006). In a second experiment, a vertical diurnal migration was implemented, making particles flip every 12 hours from 300m to 50m, as described in

160   Castonguay & McCleave (1987). This experiment mimics behaviour of eel larvae in the wild

as leptocephalus collections have been shown to have a diurnal migration depending on their length (Castonguay & McCleave, 1987). Until the length of 7mm, they are uniformly distributed over the 300m upper layers (Schmidt, 1922; Schoth & Tesch, 1983; Castonguay & McCleave, 1987). Thereafter, a diurnal vertical migration is observed from 300m in daytime and 50m at night (Schmidt, 1922; Castonguay & 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, it was decided to implement the daily vertical migration from 300m to 50m as soon as particles were released. It should be pointed out that this second experiment is considered the most realistic one.

In a third experiment, simulations allowed particles to move in the direction of fastest current velocity at each time step. The experiment may be unrealistic as there is no evidence that a leptocephalus can sense the direction and speed of a current in open water without fixed reference points. However, this experiment is a way to assess the potential impact of a different behaviour on migration duration and mortality.

THE MORTALITY MODEL: OUTLINE OF THE GENERAL METHODOLOGY

Denoting M as the instantaneous mortality rate per year, the cumulative mortality from 0 to time t is then $1-e^{-M.t}$ (e.g. Peterson & Wroblewski, 1984). For each value of M, Lagrangian simulations provide a histogram of particle migration duration d, interpreted here as a probability distribution:

$$\pi_L(d|M) \qquad (1)$$

Combined with an *a prior*i distribution for M, that was chosen as uniform on the range [0,10], a joint distribution for (M,d) can be obtained:

$$\pi_L(M,d) = \pi(M) \cdot \pi_L(d|M) \qquad (2)$$

The key idea is to combine this joint distribution with current knowledge gathered in

185 the literature to obtain a new distribution $\pi(M,d)$ confined to a more restricted range of

value of (M, d). This is achieved by the multiplication of the joint distribution $\pi_L(M,d)$ by

a second distribution independently derived from current knowledge about eel ecology (see

hereinafter) denoted $\pi_E(M,d)$:

$$\pi(M,d) = \pi_L(M,d) \cdot \pi_E(M,d) \qquad (3)$$

190 Once obtained, the marginal distribution of the migration duration d can be calculated by

integration over the possible values of M and vice versa:

$$\pi(d) = \int_d \pi(M,d)dd \qquad (4)$$

$$\pi(M) = \int_M \pi(M,d)dM \qquad (5)$$

Because the joint distribution was estimated on a discrete grid, the computation of marginal

195 distributions is straightforward.

IMPLEMENTING MORTALITY IN LAGRANGIAN SIMULATIONS

To assess how the histogram changes with M, the following procedure has been used.

The frequencies of migration duration was assessed by classes of 1 month for months

$d_i = 1, ..., n$. Let $\{f_{d_i0}\}_{i=1,...,n}$ denote the histogram formed by the frequencies, f_{d_i0}, of

200 particles with migration durations d_i obtained from Lagrangian simulation without any

mortality ($M = 0$). For each value of M, the new histogram of migration durations denoted

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$\{f_{d_iM}\}_{i=1,...,n}$ was simply obtained by weighting the initial frequency by the survival rate up to d_i:

$$f_{d_iM} = f_{d_i0} \cdot e^{-M \cdot d_i} \text{ for i in 1, ..., } n \qquad (6)$$

205   The new histogram $\{f_{d_iM}\}_{i=1,...,n}$ is then interpreted as the conditional probability distribution

$\pi_L(M,d)$, estimated on a 1-month interval grid. Lagrangian simulations are deterministic:

particles released at the same location and at the same time have the same trajectory. It could

have been possible to implement a stochastic mortality rule for each particle in the simulation.

However, as the simulations are deterministic, equation 6 provides an exact evaluation of the

210   expected mean of the frequencies in the class d_i given the instantaneous mortality M.

COMBINING KNOWLEDGE ABOUT EEL ECOLOGY

The joint distribution $\pi_E(M,d)$ can be constructed from the combination of

knowledge gathered in the literature. We rely on a steady state hypothesis. For any species

with a default sex ratio of 1:1, i.e. 50% female and 50% male, the rule 1 female gives 2

215   offspring (i.e. 1 male and 1 female) is necessary to maintain the steady state of their

population (Jung *et al.*, 2008). An equilibrium sex-ratio 1:1 was assumed for the European eel

at the population scale. Because it is a semelparous species, the steady-state hypothesis

implies that the product of the female eel fecundity by all the survival rates of their offspring

until they spawn must result in 2 individuals (Eq. 7). This equation implies that, among all of

220   the eggs produced by a female, only two individuals survive and reproduce. In this case study,

it could be formulated as:

$$2 \approx Fec \cdot \xi \cdot \alpha \cdot \beta \cdot \gamma \cdot \eta \qquad (7)$$

where *Fec* is the fecundity of female eels, ξ the hatching rate, α the survival rate of leptocephali from hatching to glass eel stage, β the survival rate of glass eels, γ the survival rate of juvenile eels (continental stage) equal to $e^{-Ma.da}$, where M_a is the annual mortality rate and d_a is the age of pre-migrating silver eels, and η is the rate of silver eels that successfully return to the Sargasso Sea and mate.

Estimates for all parameters in equation (Eq. 7) can be found in the literature, except for the parameter α, the leptocephalus survival rate and η the rate of silver eels that succeed to mate in the Sargasso Sea. Equation 7 enables us to express α as a function of the other parameters:

$$\alpha \approx \frac{2}{Fec \cdot \xi \cdot \beta \cdot \gamma \cdot \eta} \qquad (8)$$

Regarding literature data (Table I), the following values were selected: *Fec*= 1.5 .10^6 eggs, hatching survival rate= 20%, glass eel survival rate= 10%, $M = 0:14$, age of mature eels= 10 years and survival rate during the spawning migration = 30% (estimated from a 0.5 year migration duration to reach the Sargasso Sea and a high mortality rate of 0.7).

[Table I about here.]

To account for uncertainties about these point estimates, a probability distribution was assigned to each parameter (Fig. 2). Beta distributions were set for ξ, β, M_a, and γ as they range between 0 and 1. Gamma distributions were set to the fecundity (*Fec*) and the age of spawners (d_a) as these parameters have to be positive. These different distributions were combined as in Eq. 8 to provide the uncertainty about the survival rate of leptocephali.

[Figure 2 about here.]

From equation 8, an expression of the migration duration d (time for eel larvae to reach 20ºW)
can be derived given the instantaneous mortality of eel larvae M. Indeed, α is a survival rate
and can be written as $\alpha = e^{-M.(d+drem)}$, where M is the natural mortality of leptocephali and
$d+d_{rem}$ is the total duration from hatching to glass eel reaching the coast. This total duration is
the sum of the migration duration to 20ºW (d) and the time needed to reach the continental
slope and metamorphose, d_{rem}. The metamorphosis is estimated to take between 1 and 3
months (Lecomte-Finiger, 1992; Wang & Tzeng, 1998; Arai $et\ al.$, 2000; Wang & Tzeng,
2000).

One to two months were arbitrarily added to account for the time to reach the
continental shelves and cover the 1000 to 1500km remaining although it is difficult to
estimate since the larvae can arrive from Ireland (1000km from the 20°W) to Norway
(2500km from the 20°W). This estimation stems from the mean speed of currents in that area
that is about 0.2 m sec^{-1} (Fratantoni, 2001). To cover 1000 km directly with a mean speed of
0.2 m sec^{-1} would take 58 days. Thus, d_{rem} was considered to be uniformly distributed between
2 to 5 months (time to reach the continental slope and metamorphose). The following
expression can be derived:

$$e^{-M \cdot (d+d_{rem})} \approx \frac{2}{Fec \cdot \xi \cdot \beta \cdot e^{-M_a \cdot d_a} \cdot \eta} \qquad (9)$$

that gives

$$d \approx \frac{\log(\frac{2}{Fec \cdot \xi \cdot \beta \cdot e^{-M_a \cdot d_a} \cdot \eta})}{-M} - d_{rem} \qquad (10)$$

Using Monte Carlo simulations, Eq. 10 was used to derive a sampling based estimation of the conditional probability of d given M, that is $\pi_E(M|d)$. Combined with a uniform distribution on M, we obtained the joint distribution $\pi_E(M,d)$ that is needed to be combined with the Lagrangian distribution $\pi_L(M,d)$.

SENSITIVITY ANALYSIS

The two distributions $\pi_L(M,d)$ and $\pi_E(M,d)$ were combined (i.e. multiplied) to obtain the final joint estimation of the mortality M and migration duration d. To assess the soundness of results, the elasticity of $\overline{d}$, the geometric mean of the marginal distribution of the migration duration d, and $\overline{M}$, the geometric mean of the marginal distribution of the annual mortality M were calculated regarding the different parameters (Table I). Elasticity is the ratio of the proportional change in one variable with respect to proportional change in another variable. It illustrates the relative change of $\overline{d}$ and $\overline{M}$ when a parameter increases by a small percentage (here, 10 %) and when all other parameters are kept at their standard values.

RESULTS

ESTIMATION OF THE LEPTOCEHALUS SURVIVAL RATE

The probability distribution of leptocephalus survival rate (α) obtained from Monte Carlo simulations has a lognormal distribution. A point estimate (geometric mean of the distribution) for the leptocephalus survival rate is found near 0.15% (Fig. 3).

[Figure 3 about here.]

DISTRIBUTION, DEPTH-DRIFT, AND DEPARTURE AREA AND MONTH OF SIMULATED PARTICLES

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The majority of particles arriving at 20°W were distributed between 40 and 55°N, with a peak at 50°N (Fig. 4). Another peak appears in the North Africa area (30-35°N). A more northerly peak was also observed (57-62°N). The migration pathways follow the Gulf Stream and North Atlantic drift (Fig. 5). Some particles that drifted more than 2 years followed the

290 Azores Current and arrived at Moroccan latitudes (Fig. 5). It is noteworthy the majority of particles arrived at Western Europe latitudes as illustrated in Figs. 4 and 5. The main departure area of arriving particles was located in the Western Sargasso Sea (75°-65°W and 22°-30°N; Fig. 5). The same patterns of departure and arrival areas were observed for the three experiments, i.e. fixed-depth, vertical migration, or faster current choice. Regarding the

295 fixed-depth experiment, the depth range of particles crossing the 20°W was between 400m and the surface. The Gaussian distribution of these depths had a mode at 200 m. The departure month of particles that reached the 20°W without mortality was uniformly distributed over the year. The same number of particles arrived at 20°W whatever the departure month (Fig. 6, solid line). However, when applying an annual mortality rate (3.8),

300 the distribution of departure months exhibited a clear peak from March to June (Fig. 6, dashed line). For instance, three times as many particles released in April (the estimated spawning season, McCleave, 2008) reached the 20°W compared to those released in July.

[Figure 4 about here.]

ESTIMATION OF MIGRATION DURATION AND ANNUAL MORTALITY FOR

305 FIXED-DEPTH EXPERIMENTS

To illustrate overall patterns, migration durations were determined for particles released every 15 days during the year 1961 and drifting over 23 years at fixed depth, with no mortality (M=0). A histogram of the data has a log-normal shape as is usually the case for such analyses (Bodin *et al*. 2003; Wu & Hu, 2007), with a clear mode around d = 13 years (= 156 months) (Fig. 7a).

[Figure 5 about here.]

Figure 7b shows the same histogram but reduced to 0 to 5 years migration duration. The minimum migration duration was in the class 10-11 months but does not appear in Fig. 7a since there was only one particle. The distribution changed drastically when applying a mortality rate (Fig. 7c). With a mortality rate of 2 per year, the distribution of the migration duration can be estimated as in Fig. 7c. The geometric mean of this distribution was 2.4 years. An annual mortality rate equal to 2 is equivalent to a survival rate of 13.5% per year (exp(-2 . 1)). From the Lagrangian simulations, the distribution of the migration duration was estimated for each value of the annual mortality M, comprised between 0 and 10 with an incremental step of 0.2. By considering a uniform distribution on M, an estimation of the joint distribution $\pi_L(M,d)$ was obtained on a 51 x 60 grid. Figure 8a shows the contour of the joint probability distribution $\pi_L(M,d)$. The modal value was found for a short migration duration (less than 1 year) and a high annual mortality. Figure 8b shows the contour of the joint probability distribution $\pi_E(M,d)$ obtained from the combination of knowledge about eel ecology following Eq. 10. The maximum probability was found for migration durations close to 0.5 and annual mortality rate close to 10. The joint probability distribution $\pi(M,d)$ was obtained from the combination of the Lagrangian probability distribution with the distribution obtained from knowledge about eel ecology (Fig. 8c). The combination of the two sources of

information drastically reduced the uncertainty about (d, M). The new distribution $\pi(M, d)$

330   had restricted values, with modal values around the point (d = 1.5 years; M = 4 per year). The

marginal distributions of d and M show that the most credible value (i.e. the geometric mean

of the values) are 1.49 years for the migration duration and 3.8 per year for the mortality rate,

which corresponds to a survival rate of 2.2% per year (Figs. 9a and 9b).

[Figure 6 about here.]

335   LARVAL BEHAVIOUR DOES NOT INFLUENCE THE MIGRATION DURATION

Migration duration and annual mortality estimates are not very sensitive to simulations

of different larval behaviours. Implementing active behaviours for particles leads to sharper

peaks in distributions but only small ones in geometric means (Fig. 9). The geometric mean

migration duration was 1.48 years for the vertical migration experiment and 1.51 years for

340   fastest current choice (Fig. 9c and e). Comparable mean annual mortalities are 3.79 and 3.73

years respectively (Fig. 9d and f).

[Figure 7 about here.]

OCEANIC CONDITIONS INFLUENCE THE MEAN MIGRATION DURATION

Over the whole simulated years for the fixed-depth experiment, the standard deviance

345   of migration duration is 3.1 months. After removal of autocorrelation as described in Pyper &

Peterman (1998), significant negative relationships were found between the geometric mean

migration duration and the large scale oceanic indices (r = -0.51, p < 0.05 with the NAO

index, r = -0.51, p < 0.01 with the Gulf Stream Index, and r = -0.46, p < 0.05 with the

Transport Index). The higher the oceanic indices, the lower the mean migration duration.

350   Similar results are found with the two other behaviour hypotheses.

[Figure 8 about here.]

SENSITIVITY ANALYSIS TO PARAMETERS

Elasticities of the mean migration duration and larval mortality were both low (Table

II), indicating that changes in one parameter, considering the others as fixed, has a low impact

355   on results. For instance, if ξ increases by 10 %, the mean migration duration estimated in Exp.

1 will increase by 7 %. These results are consistent with Eq. 9. If the hatching rate increases,

the survival rate of leptocephali decreases to maintain the steady state of the population. The

same conclusion applies for the mean migration duration. If the survival rate of glass eel

increases, one solution to maintain the steady state of the population is to increase the time of

360   exposure to leptocephalus mortality, as expressed by Eq. 9. The sign of elasticity is positive

and therefore consistent with the steady-state hypotheses. Furthermore, given the same

experiment, elasticities should have been strictly equal for parameters that have the same role

in Eq. 9, i.e. Fec, ξ, β, and η or M_a and d_a. The small differences stem from the numerical re-

simulations of these different parameters when adding a small variation.

365   [Figure 9 about here.]

DISCUSSION

ESTIMATES OF THE MIGRATION DURATION

To provide accurate estimates of migration duration, larval mortality has to be accounted for in Lagrangian studies. The longer that particles drift, the more particles arrive to the 'finishing line'. Without accounting for mortality, the mean migration duration from the Sargasso Sea spawning area to 20ºW ranges from 11 to 15 years. Cowen *et al*. (2000) and Hare *et al*. (2002) have similarly shown the importance of accounting for mortality in simple advection models. Taking mortality into account, the geometric mean migration duration to reach 20 º W is about 1.5 years. The time for leptocephali to reach the continental slope and metamorphose into glass eels has still to be accounted for. Glass eels may also have to wait for an increase in water temperatures before migration into estuaries can begin. These delays were not taken into account because they are highly variable and depend on local and interannual variability in water temperature.

[Table II about here.]

The duration of the migration from 20°W to the continental shelf was estimated as the sum of two phases, the first being the time taken to reach the continental slope where leptocephali are believed to metamorphose into glass eels. The second phase was the time lag between metamorphosis and entry to estuaries (estimated by otolith microstructure). The distance between 20°W and the closest coast, *i.e.* the coast of Ireland, is 1000 km and current speeds in that area are about 0.2m sec^{-1} (Fratantoni, 2001), thus the minimum time to cover this distance is thus 58 days. This distance and duration can obviously vary greatly, resulting in differences in diffusion and time-related mortality - reflected in times of arrival (Tesch, 2003) and clines in relative levels of recruitment (e.g. Bark *et al*., 2007). Published estimates for the length of metamorphosis phase are about 98 days, 33-76 days and 18-52 days, according to Wang & Tzeng (1998, 2000), Lecomte-Finiger (1992) and Arai *et al*. (2000)

respectively. Thus, 1 to 3 months have to be added to the migration duration to account for the metamorphosis into glass eel as well. The migration duration is therefore at least 21 months (18 months to cover the distance to 20ºW and 3 months to cover the distance from 20°W to European shelves and metamorphose into glass eel).

395   Observations of the occurrence of leptocephali in the Sargasso Sea from February to June and main arrivals on European shelves from December to April imply that the migration duration is about 11 months or modulo 11 months (Kettle & Haines, 2006). The 21-month migration duration proposed in this paper is consistent with this time lag between spawning and arrivals (McCleave, 2008). Results are not in agreement with otolith microstructure

400   studies and it is possible that leptocephali may have such a low metabolic rate that increments in otoliths might not be deposited daily, especially at low temperature, or may be deposited daily but are too thin to be observable in either light or scanning electronic microscopy (Bonhommeau *et al*., submitted).

Powles *et al*. (2006) demonstrated that increment formation during metamorphosis was daily

405   in the speckled worm eel (*Myrophis punctatus*), but otolith growth has been observed to be strongly affected by temperature below 10°C in *A. japonica* glass eels by Fukuda *et al*. (2009). The reliability of the different methods used to estimate migration duration remains controversial. Two hypotheses are currently proposed. Otolith microstucture results estimate a short migration duration (=< 1 year, Lecomte-Finiger, 1994; Wang & Tzeng 1998) and cohort

410   analysis, otolith macrostructure, and particle-tracking models estimate a longer migration duration (>1.5 years, Schmidt, (1922) ; van Utrecht & Holleboom (1985), Kettle & Haines (2006)). The present results are in agreement with longer migration duration estimates.

        Passive drift of eel larvae was assumed in this work. Active migration has been suggested to explain the shorter transit times derived from otolith microstructure analyses.

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415　However, Bonhommeau *et al*. (accepted) estimated the swimming speed of leptocephali would need to be at least 3.4 body lengths sec^{-1} to cross the Atlantic Ocean in six months. The swimming hypothesis also seems unlikely because of low food availability in the open-ocean and the energy cost of swimming (McCleave *et al*., 1998). Uncertainties about leptocephalus diet and behaviour in the wild need clarifying to improve simulation designs and

420　understanding of the oceanic phase of eels.

ESTIMATES OF THE NATURAL MORTALITY ARE LOWER THAN IN OTHER FISH SPECIES

　　　Reliable estimates of natural mortality, especially during the early-life stages, are critical in stock assessment, recruitment forecasting and management of fish species.

425　However, estimates of natural mortality rates of fish vary widely between and within species (McGurk, 1986). For instance, the natural larval mortality of European plaice (*Pleuronectes platessa*), Atlantic cod (*Gadus morhua*) and Atlantic mackerel (*Scomber scombrus*) are estimated at 0.02, 0.16 and 0.69 per day respectively (Bannister *et al*., 1974; Ware & Lambert, 1985; Kristiansen *et al*., 1997). In the present study, natural mortality of

430　leptocephali is estimated to be 3.8 per year (about 0.01 per day), lower than other fish larvae. Most fishes have a short larval stage, from a few weeks to a few months, and applying a natural mortality rate to eel larvae of the same magnitude as other pelagic larvae would make it impossible for them to effectively cross the Atlantic. This result is therefore difficult to compare to other fish species. To the authors' knowledge, no study has ever provided an

435　estimate of natural mortality of eel leptocephali for comparison with other estimates. Kettle & Haines (2006) found that of 1.6×10^6 drifters released, 0.66% arrived at 25°W within 2 years. Actually, Kettle & Haines (2006) tacitly induced a mortality hypothesis since their

simulations were stopped after two complete years, i.e. equivalent to a survival rate of 100% up to two years and 0% thereafter. However, the 0.66% value is not a survival rate since no realistic mortality rate was implemented in their model. The estimate of a 3.8 annual mortality rate over 21 months is equivalent to a survival rate of 0.18% larvae and is consistent with the steady-state hypothesis of the population (Eq. 7 and Fig. 3). It is also consistent with observations of glass eel arrivals. The European eel spawning season is estimated to be from February to June and mostly concentrated from March to May (Schmidt, 1922, McCleave & Kleckner, 1987, McCleave, 2008). If the natural mortality rate was very high, leptocephali that spend too much time in the Atlantic Ocean would die. This would lead to selection of individual that cross the Atlantic quickly and the migration duration would be short and the arrival dates in continental waters would form a narrow peak. This result does not correspond to observations of the seasonality of glass eel arrivals (McCleave, 2008). For instance, glass eel fishing in the Bay of Biscay is generally concentrated between November and April depending on the distance from the edge of the continental shelf. However, catches from illegal fishing done outside the fishing season provide a substantial amount of glass eel even during July and August. For these latecomer leptocephali, it implies a more prolonged sojourn in the Atlantic Ocean as well as a longer migration that would not be possible if the mortality rate was very high.

As a result, a higher mortality rate during larval stage than during next stages has been found which is consistent with general considerations about the importance of this specific period (e.g. Levin & Stunz, 2005).

BEHAVIOUR HYPOTHESES HAVE A WEAK IMPACT ON MEAN MIGRATION DURATION AND MORTALITY ESTIMATES

Mean migration duration and annual mortality do not seem to be greatly influenced by the behaviours simulated. However, the distributions of migration durations have more pronounced modes for the experiments with vertical diurnal migration and faster current choice (Fig. 9). This actually could be an artefact induced by the Lagrangian simulations. For these two experiments, fewer particles were released than for the fixed-depth experiment. In the fixed-depth experiment, particles were released at each vertical mesh level (26 levels), but this was not necessary for simulations involving the two other behaviour hypotheses. For instance, regarding the fastest current choice behaviour, all particles starting at the same horizontal position would have chosen the same depth levels at the first time step and so on. The same applies to the vertical diurnal migration since depths are fixed at 300m during the day and 50m at night. Consequently, once the first particle has arrived, some time-classes have a low number of particles or none at all for these two behaviour experiments. When applying a mortality rate, the first particle was selected and had a high probability in the joint distribution of M and d but the next particles had very low or null probability. When multiplying the two joint distributions, i.e. Lagrangian results ($\pi_L(M,d)$; Fig. 8a) and steady-state hypothesis ($\pi_E(M,d)$; Fig. 8b), the joint probability ($\pi(M,d)$) of the first particle was therefore high compared to the other. This helps explain the pronounced mode for experiments with vertical migration and the fastest current choice. Nevertheless, the range of values between the different experiments is similar and suggests that the behaviours modelled do not significantly minimise migration duration. Vertical diurnal migration is probably a way to avoid predation and optimise foraging, as is the case for other zooplankton (Steinberg *et al*., 2002), rather than a strategy to accelerate larval drift.

INFLUENCE OF OCEANIC FEATURES ON EUROPEAN EEL RECRUITMENT

The negative correlations detected between the mean migration duration and oceanic conditions represented by the NAO index, the Transport Index and the Gulf Stream Index are predictable, since when these indices are high, mid-latitude westerly winds are intensified over the North Atlantic and currents are faster. For example, when the NAO is high, a larger number of particles will successfully cross the Atlantic, because the migration duration is shorter and hence mortality is lower. However, all these indices were relatively low before the 1980s and increased steadily until the mid-1990s. The period 1980-1995, when oceanic conditions were apparently more favourable regarding the migration duration and hence survival, was paradoxically the period when the decline in eel recruitment began. Three non-exclusive hypotheses may explain this apparent anomaly: either the high indices are also related to strong mesoscale eddies that may trap particles, but are not resolved in the ocean general circulation model used, or the physical oceanic conditions such as current speeds may not affect the recruitment success. The latter means that the negative relationships found between NAO and eel recruitment indices (Knights, 2003; Friedland *et al*., 2007) do not correspond to the signal of physical oceanic conditions described by the NAO. The NAO is indeed an integrative index and is related to a large number of physical but also biological features (Hurrell, 1995; Fromentin & Planque, 1996; Straile & Stenseth, 2007). As the NAO is negatively correlated to primary production in the Sargasso Sea (Bates, 2001), the negative relationship between NAO and recruitment could be linked to biological production in the eel spawning area as showed by Bonhommeau *et al*. (2008). Ocean general circulation models that resolve mesoscale and sub-mesoscale eddies could be used to determine whether the same patterns of migration durations can be found and whether the ocean circulation has a direct impact on eel leptocephali survival. The use of high resolution models has been initiated for the Japanese eel (Kimura *et al*.; 1994; Kim *et al*., 2007). A third hypothesis is

that anthropogenic adverse effects started seriously interfering with eel recruitment in the early 1980s, regardless of oceanic conditions.

510   With regards to steady-state hypotheses, Eq. 7 describes the necessary conditions for a species to maintain its population. This equation applies when the parameters used are those of the population at steady-state. However, cyclic fluctuations in levels of recruitment and stocks have been observed and make it difficult to determine what a steady state is. To overcome this problem, parameters given in the literature when the population was fluctuating

515   around a mean and showing no clear trends have been favoured (before the decline in the 1980s).

Regarding the current decline of European eel, Eq. 7 is clearly false since one female does not produce two individuals able to spawn (see depletion rate estimated by Åström & Dekker, 2007). However, this study aimed at estimating the natural mortality and migration duration

520   of leptocephali. The assumption was made that natural mortality and migration duration are not influenced by factors affecting the European eel during its continental life stages such as overfishing, pollution, habitat loss, etc. This assumption is also conceptually false since, for instance, fishing may select glass eels arriving in European rivers before or after the fishing season. Thus, individuals that have a shorter or longer migration duration may be genetically

525   favoured. However, the authors consider that it is currently impossible to assess the evolutionary effects of fishing, pollution, etc. on eel larval migration. This assumption (based on and extending Eq. 9) can be written as:

$$e^{-M \cdot t} \approx \frac{2}{Fec \cdot \xi \cdot \beta \cdot e^{-M_a \cdot d_a} \cdot \eta} \approx \frac{X}{Fec \cdot \xi \cdot \beta \cdot e^{-M_a \cdot d_a} \cdot \eta \cdot \prod_i \delta_i} \quad (11)$$

where X is the current number of spawners produced by a female, δ_i are all other survival

530   rates induced by the impact of overfishing, habitat loss, pollution, climate, etc. on the eel. It

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was thus assumed that factors inducing the current decline in eel population have no effect on migration and larval mortality. When using only Lagrangian simulations where the eel population was assumed to be at steady-state (i.e. before the decline in the 1980s), the same mean migration duration and mortality was obtained (data not shown). This reinforces the idea that using a steady-state hypothesis is an appropriate first assumption to estimate the mean migration duration and larval mortality. The last hypothesis that has been made when assuming that one female produces two individuals able to spawn is that the sex ratio is 1:1. This hypothesis may be wrong but currently there is no way of estimating the overall sex ratio of the European eel throughout the species range.

In conclusion, Lagrangian simulations coupled with mortality hypotheses have allowed the estimation of the trans-Atlantic migration duration and the natural mortality of European eel leptocephali. Results show the importance of accounting for mortality in Lagrangian modelling of the duration of fish larval migrations. In particular, with a mortality hypothesis a strong influence of the departure month is revealed. It could be hypothesized that a temporal determinism of the spawning season stems from physical oceanography. The European eel population can maximize larval migration success (i.e. minimize the migration duration) when spawning from March to June, due to favourable currents over this period (Fig. 6). The mean migration duration is estimated at 21 months, longer than estimates derived from otolithometry, but shorter than those from cohort and other analyses. Estimated larval mortality is low compared to other fish species, i.e. an annual mortality rate of 3.8 (equivalent to a survival rate of 0.12% over the migration). Allowing for different leptocephalus behaviours did not appear to have an influence on simulated mean migration duration and mortality. Environmental indices indicative of changes in transport currents do not seem to be related to the post-1980s decline in glass eel recruitment, since they appeared

555   to be more favourable (lower migration duration) when recruitment declined. These results

may be influenced by the resolution of the ocean model in use and improvements have to be

considered in future work. Lagrangian simulations appear to be a promising way to

understand the migrations and early life history of eels and the use of higher resolution ocean

general circulation models will help. The implementation of a decreasing mortality rate of

560   larvae with time and growth in size could be a further improvement as the mortality rate of

fish larvae is known to decrease with increasing size (Cushing, 1974; Pearcy, 1984). The

online coupling of Lagrangian simulations and mortality of larvae would also be informative.

These results fit with the unique developmental strategy of eel larvae to achieve their

migration over long distances in open-oceans of low productivity. The ability of eel to adapt

565   to different environmental conditions, i.e. its plasticity, allows it to colonize a wide-spectrum

of habitat from the Arctic polar circle to the shelves of Morocco. Moreover, the low mortality

of leptocephali in the open ocean, demonstrated in the present work, allows them to survive

major variations in oceanic circulation. Nevertheless, high amplitude and very long-term

variations of oceanic circulation have had a strong impact. The Wisconsin (20000 BP) or

570   Younger Drias (12000 BP) glaciations have resulted in a strong reduction of the speed of the

Gulf Stream (Lehman & Keigwin, 1992; Keigwin & Jones, 1994; Duplessy, 1999; Lynch-

Stieglitz *et al*., 1999; Rahmstorf, 2002). In turn, this decrease in the speed of the Gulf Stream

may have initiated declines in eel recruitment (Wirth & Bernatchez, 2003) and a

concentration in restricted areas (Kettle *et al*. 2008b). Eels appear indeed to have maintained a

575   continuous presence in southern Europe throughout the last glacial period while they were

absent from northwestern Europe north of the Gironde drainage basin (Kettle *et al*. 2008b).

Regarding the current decline in eel recruitment, one of the major questions is the potential

effects of global warming and its consequences on global circulation. If eels adopt the strategy

of restricting themselves to specific areas depending on ocean circulation (e.g. in the

580   Mediterranean and the Atlantic coast of western Europe, as during glaciation events), this may

have strong implications in terms of management. In particular, this raises questions about the

future benefits of stocking in the northern part of the species distribution.

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choice experiments, (b) the annual mortality estimated using Eq. 10 for the fixed depth
experiments, (d) the vertical migration experiments and (f) and the faster current choice
experiments.

Figure 1: Map of the initial positions for the Lagrangian simulations using the Drakkar model (i.e. each 1/4°) and the location of the European eel spawning area (polygon; redrawn from McCleave *et al.*, 1987). The upper right panel shows the 20°W migration 'finishing line' in the Atlantic Ocean.
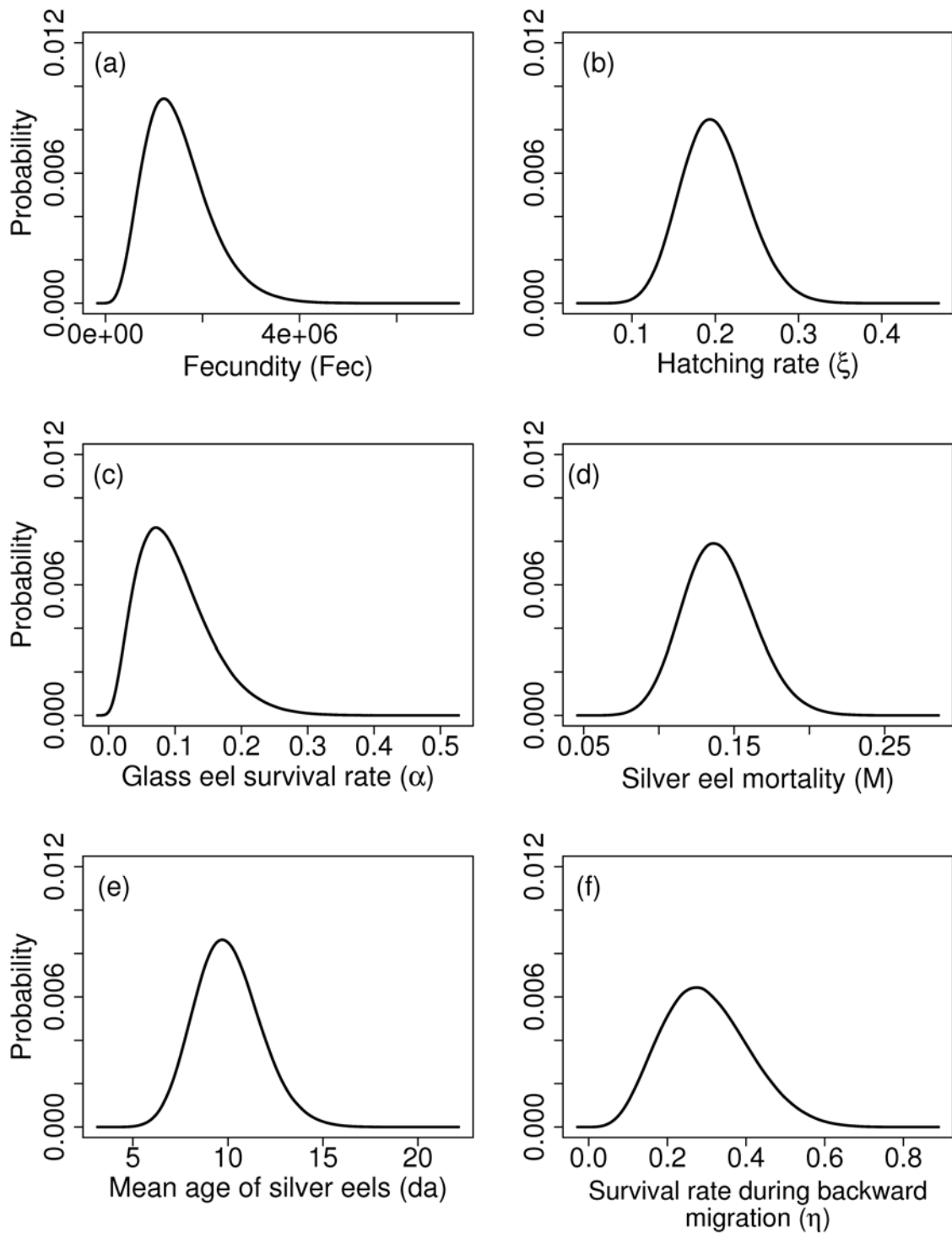
Figure 2: Probability distribution of the different parameters used to calculate the survival rate of leptocephali.
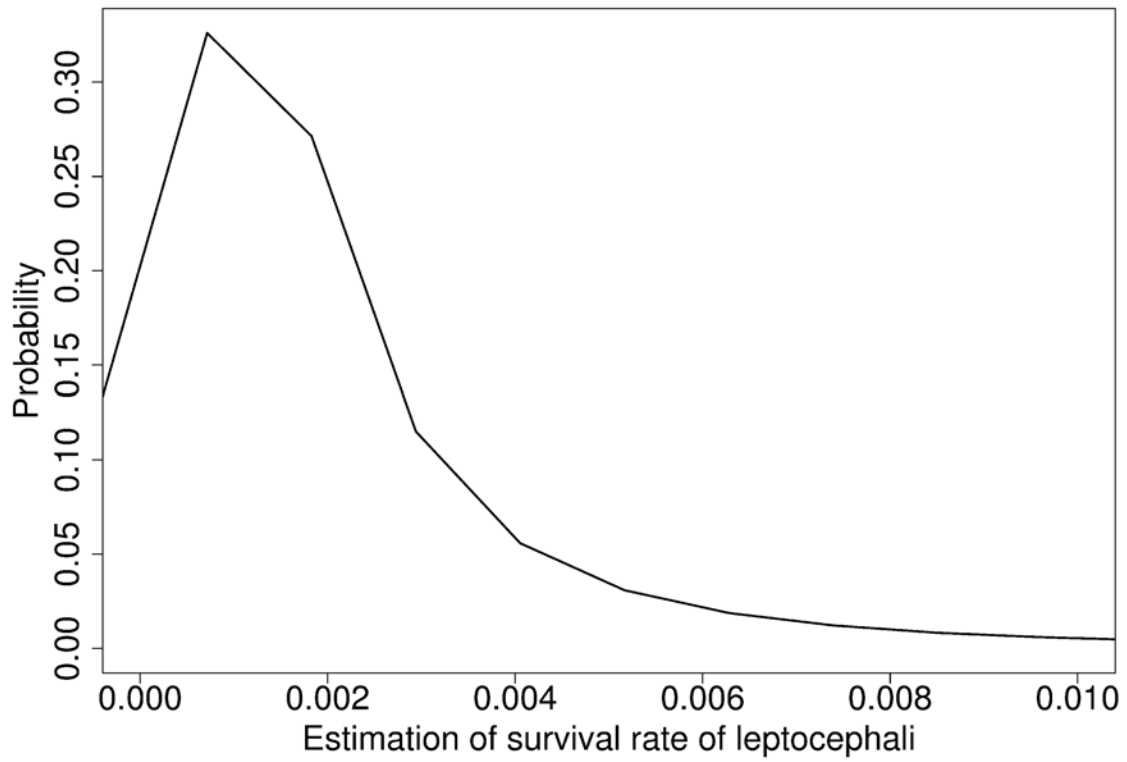
igure 3: Probability distribution of leptocephali survival rate accounting for uncertainties in the values for different parameters in Eq. 7 gathered from the literature.
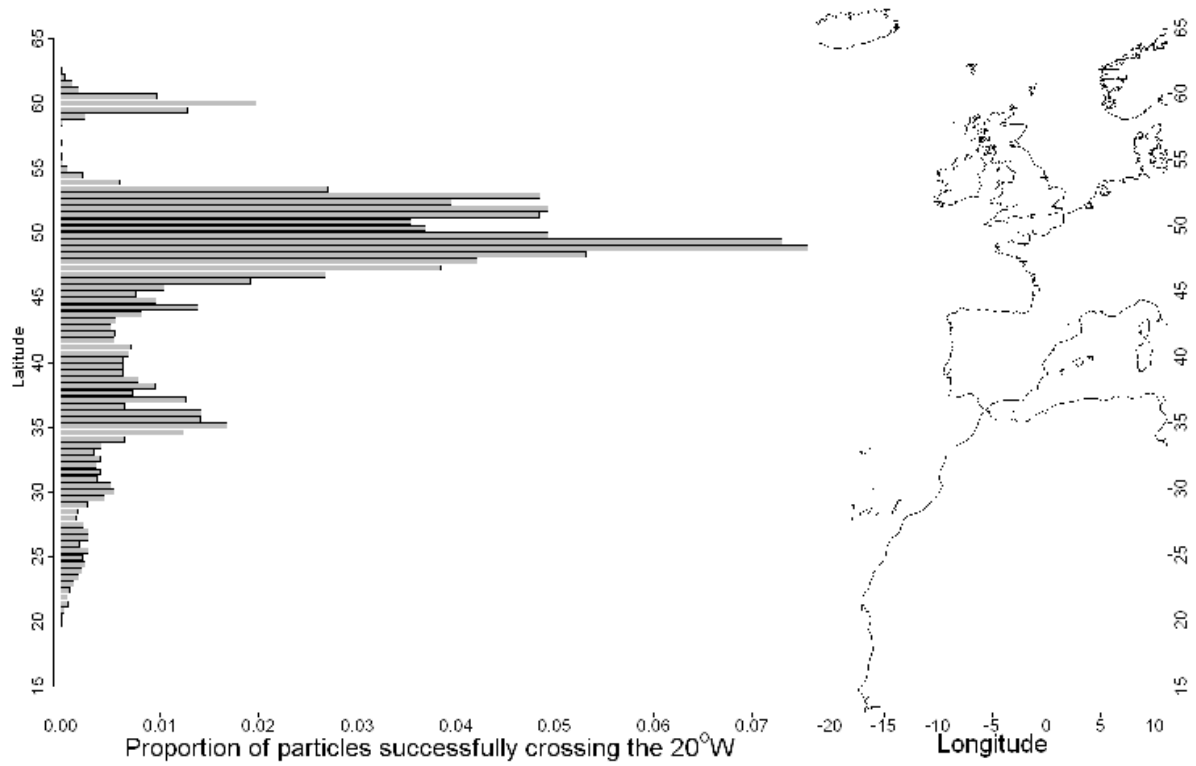
Figure 4: Proportion of particles successfully crossing the 20ºW meridian at different latitudes. Particles were released over 5 years within the eel spawning area and simulations allowed for vertical diurnal migration. The map on the right hand side shows the location of the latitude bins defining the histogram and is drawn up to the 20ºW where particles were counted.
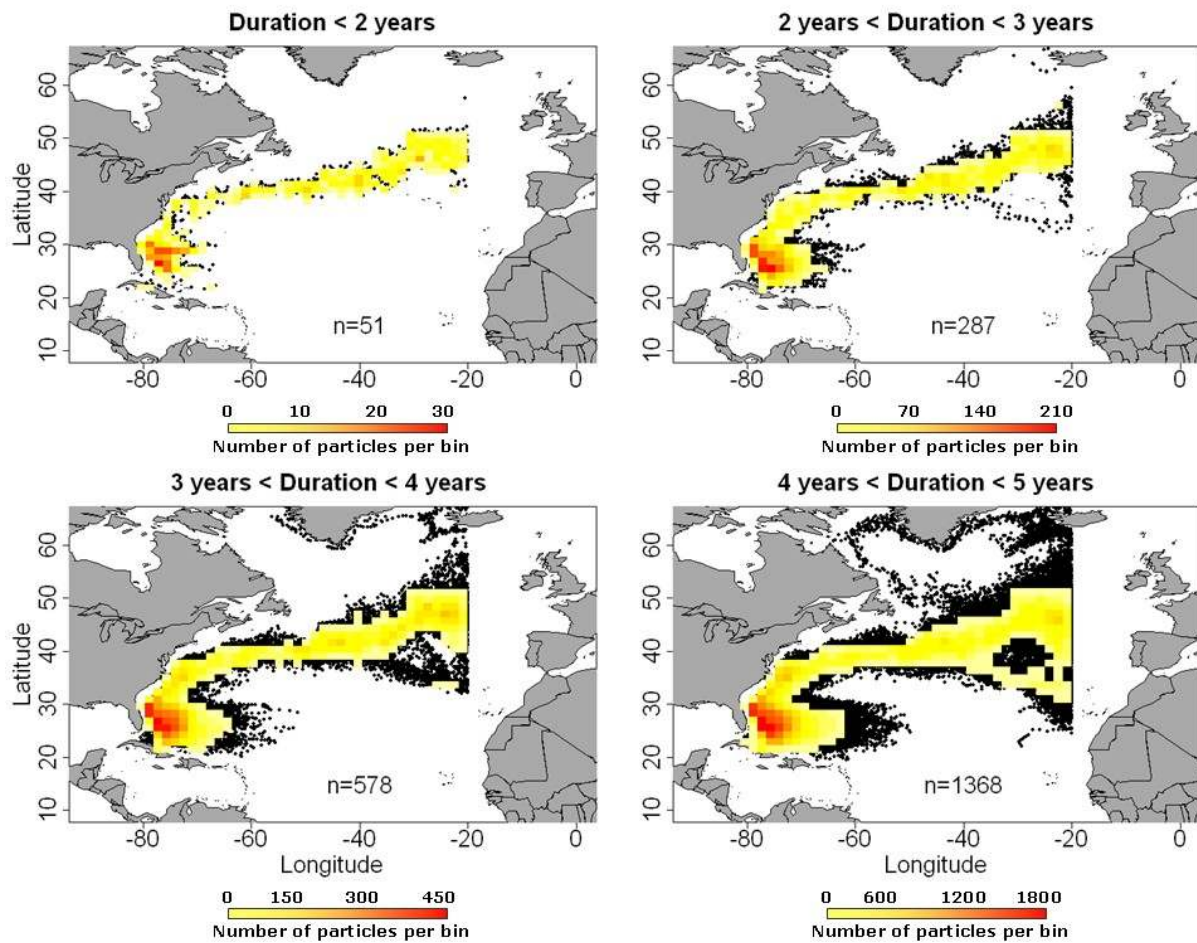
Figure 5: Trajectories of all the particles released in the eel spawning area and successfully crossing the 20ºW meridian. Particles were tracked over 5 years and undergo a vertical diurnal migration from 50m at night to 300m during the day. Colour scale represents the density (number of particles that entered a box) in each bin defined as a 1° longitude x 1° latitude box. *n* is the number of particles that succeeded to reach the 20°W over the period defined in panel title.
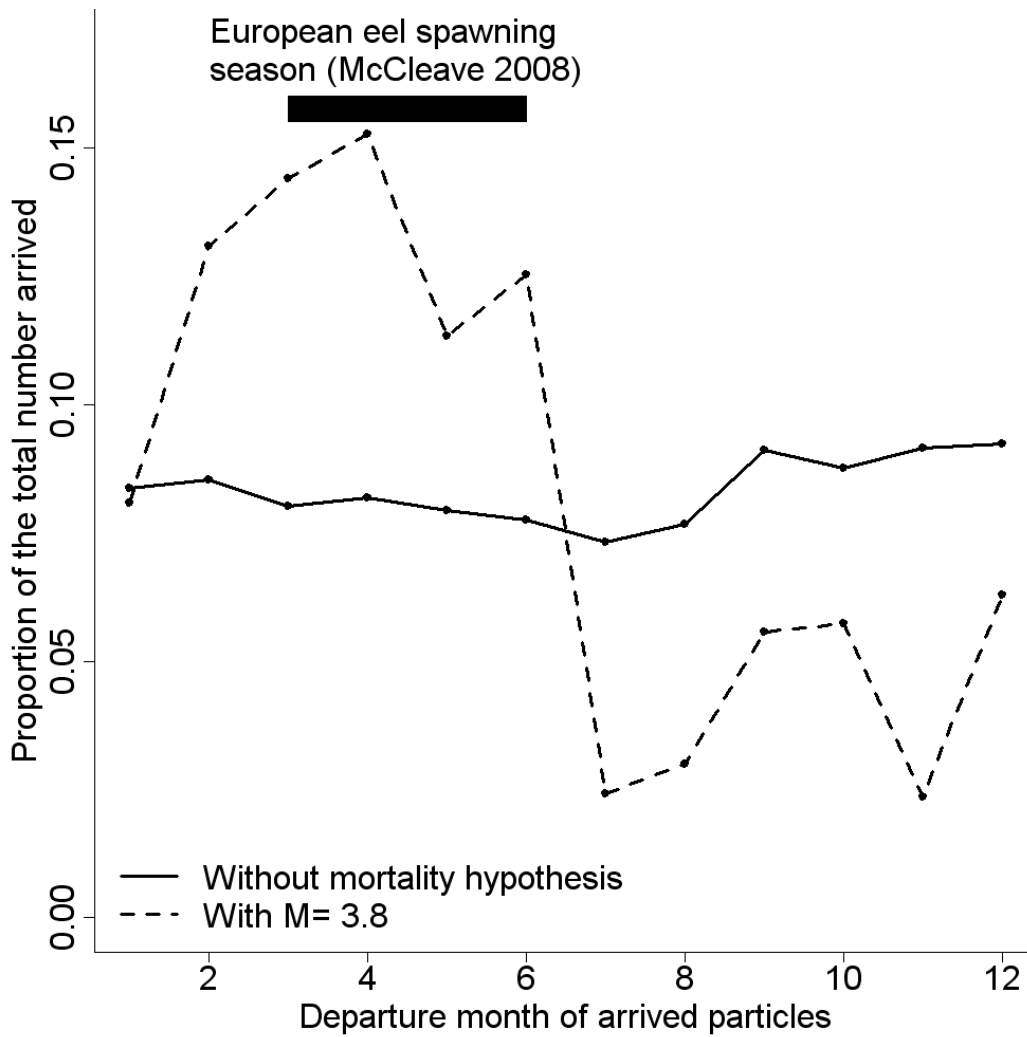
Figure 6: Proportion of particle released in the eel spawning area and that reached the 20°W for each departure month (from January (1) to December (12)). Particles were tracked over 5 years and undergo a vertical diurnal migration from 300m at night to 50m during the day. 860 Solid line represents the proportion without a mortality hypothesis and dashed line, with a annual mortality rate (3.8) hypothesis. The black rectangle is the estimated spawning season for the European eel.
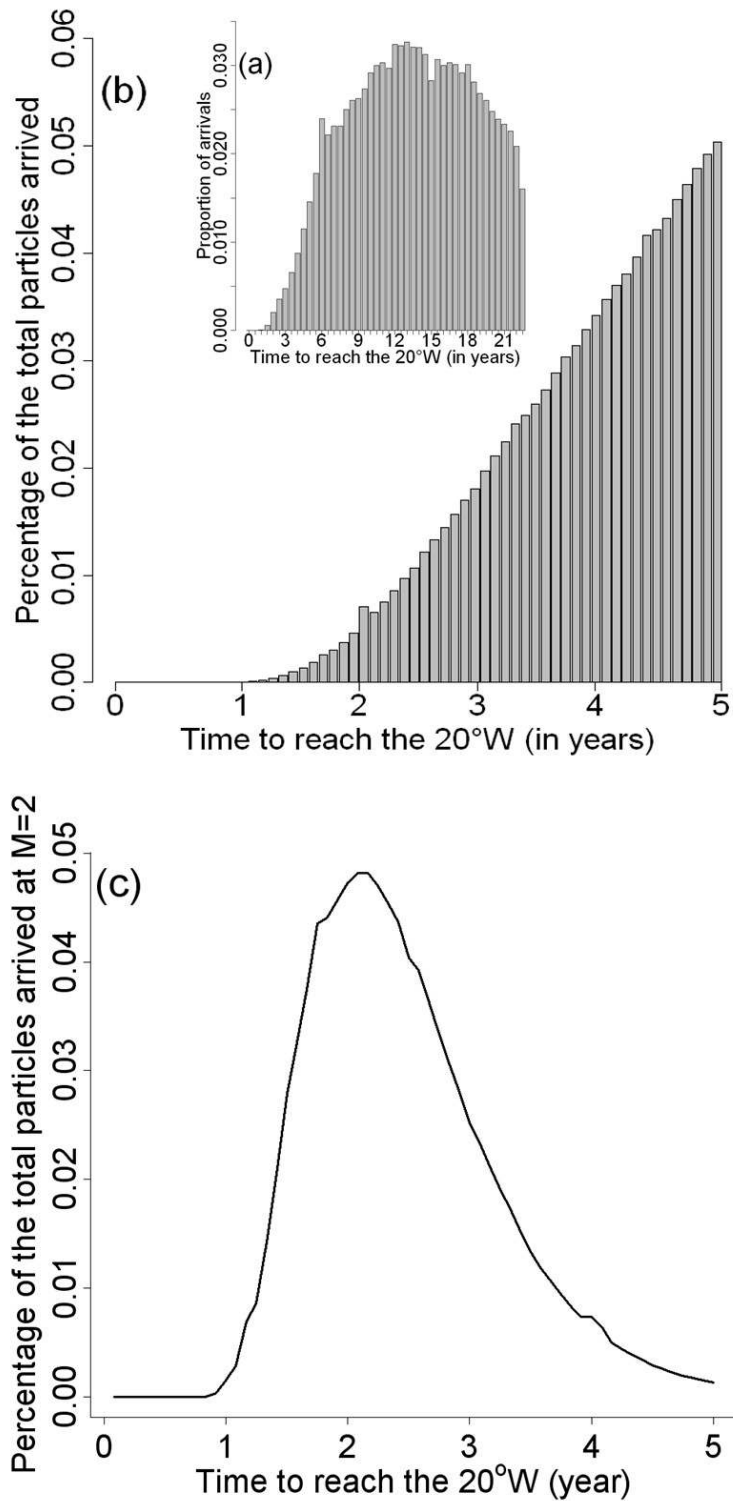
Figure 7: (a) Histogram of the time needed to reach $20°W$ for particles released in the
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classes (b) The same histogram truncated at 5 years. (c) Plot of the same histogram when
applying an annual mortality (M) of 2. Figures used results of the fixed-depth experiment.
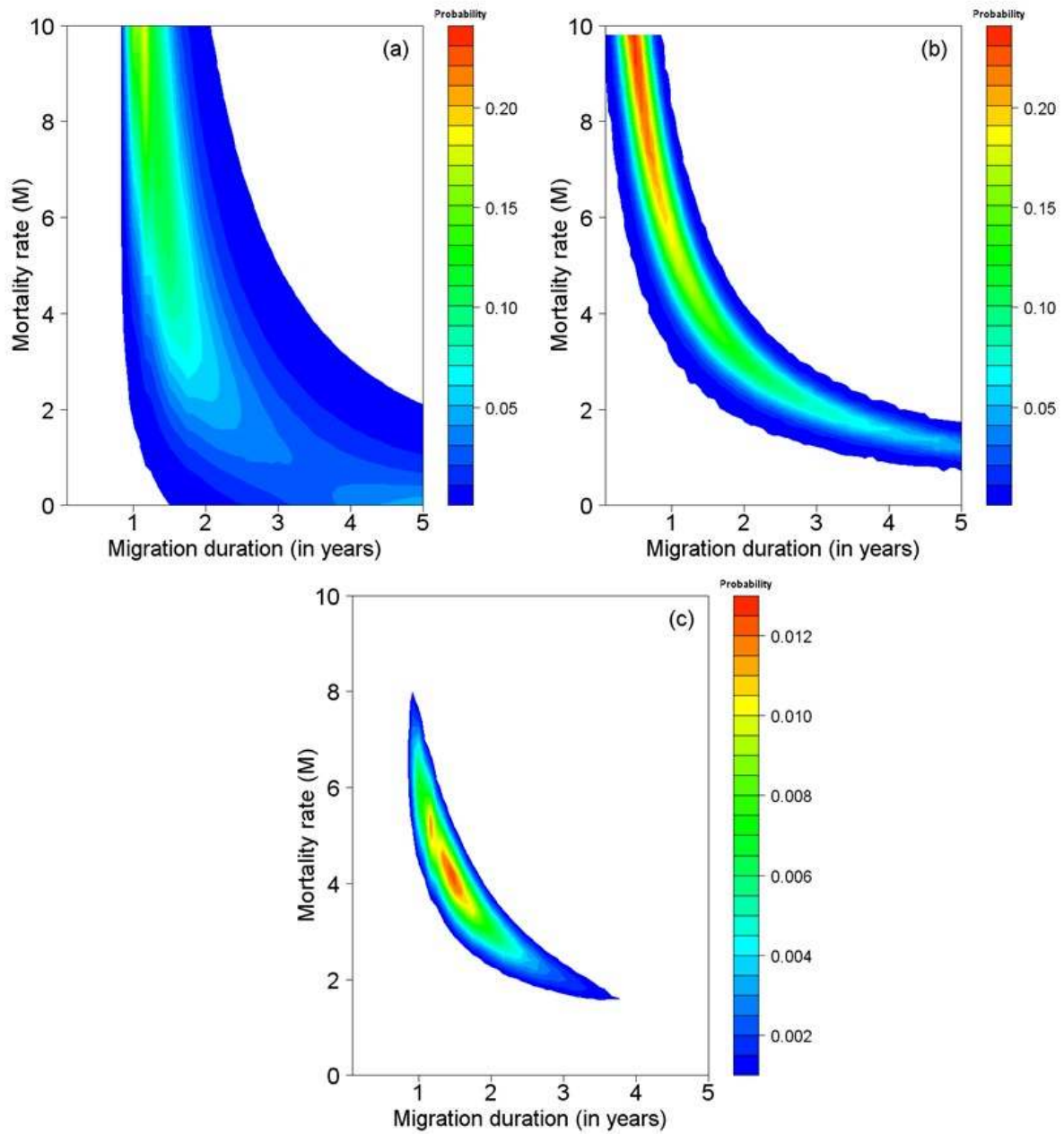
Figure 8: (a) Probability distribution of the migration durations estimated by Lagrangian simulations for different annual mortalities (denoted $\pi_L(M, d)$ in the text). This figure shows the results of experiments at fixed-depth. (b) Probability distribution of migration durations estimated by the steady state hypothesis of the population (see Eq. 10) for different annual mortalities (denoted $\pi_E(M, d)$ in the text). (c) Intersection of the probability distribution of migration durations estimated by the steady state hypothesis of the population and by the Lagrangian simulations (denoted $\pi(M, d)$ in the text)
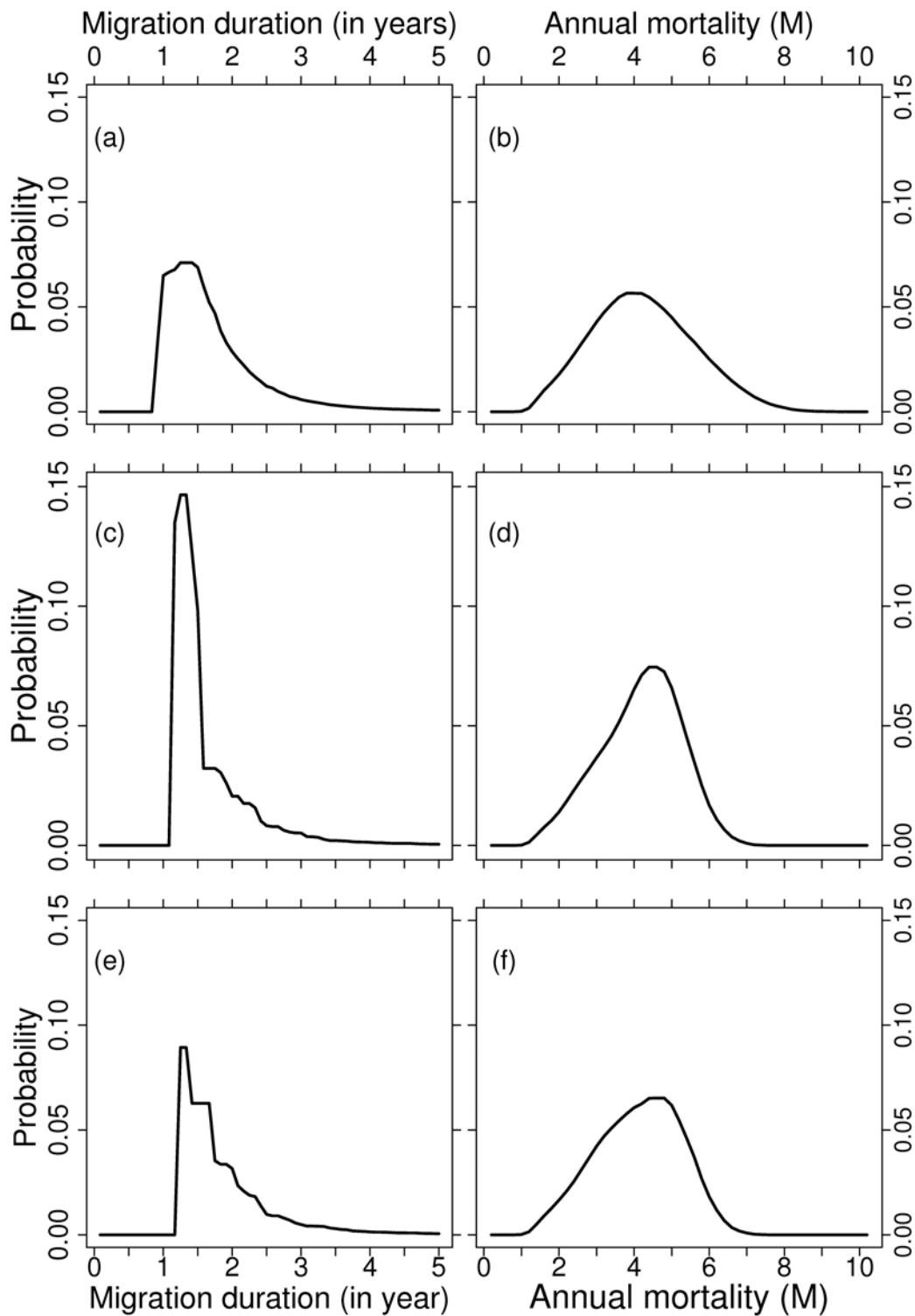
Figure 9: Marginal distributions of the migration duration estimated using Eq. 10 for (a) the fixed depth experiments, (c) the vertical migration experiments, (e) and the faster current choice experiments, (b) the annual mortality estimated using Eq. 10 for the fixed depth experiments, (d) the vertical migration experiments and (f) and the faster current choice experiments.

List of Tables

Table I. Estimates of the different parameters given in Eq. 7. *Fec* is the fecundity of female eels (number of eggs per individual), ξ the hatching rate, β the survival rate of glass eels, γ the survival rate of adult eels (continental stage) that equals to $e^{-M_a.d_a}$, where M_a is the mortality rate and d_a is the age of silver eel before seaward migration, and η is the rate of silver eels that succeed in crossing the Atlantic Ocean and mating.

Table II. Elasticity of the estimated mean migration duration and mortality regarding the different parameters given in Eq. 4.2 for each experiment. Symbols as in Table I.

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Parameter	Range of value	Source
Fec (# of eggs)	$9.10^5 – 2.6.10^6$	Boëtius & Boëtius (1980)
	1.10^6 (55cm), $4 - 5.10^6$ (95cm)	B. Knights (pers. comm.)
	$1.49.10^6$ ($9.10^4 – 6.10^6$) (39-99cm)	Bark *et al*. (2007)
ζ	10-30%[a]	Furuita *et al*. (2003)
	20-40%[a]	Unuma *et al*. (2004)
β[b]	17.3-23.1%	Berg & Jorgensen (1994)
	3-27%	C. Briand (pers. comm..)
	26-32%	Moriarty & Dekker (1997)
M_a	0.14 per year	Dekker (2000)
d_a	2-20 years	Tesch (2003)
	8-18 years	Bertin (1956)
η	30%	-

[a] estimates for the Japanese eel
[b] for the stage

Table II: Elasticity of the estimated mean migration duration and mortality regarding the different parameters given in Eq. 4.2 for each experiment. Symbols as in Table I.

Variable and simulation design	Fec	ξ	β	M_a	d_a	η
Mean migration duration						
Exp. 1 (fixed-depth)	0.07	0.07	0.07	-0.16	-0.16	0.07
Exp. 2 (vertical migration)	0.06	0.05	0.05	-0.11	-0.11	0.05
Exp. 3 (fastest current choice)	0.06	0.04	0.05	-0.12	-0.12	0.05
Mortality						
Exp. 1 (fixed-depth)	-0.24	-0.22	-0.22	0.49	0.49	-0.22
Exp. 2 (vertical migration)	-0.22	-0.19	-0.20	0.45	0.45	-0.20
Exp. 3 (fastest current choice)	-0.23	-0.21	-0.20	0.46	0.46	-0.21

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