Modeling the drift of European (*Anguilla anguilla*) and American (*Anguilla rostrata*) eel larvae during the year of spawning

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1 **Modeling the drift of European (*Anguilla anguilla*) and American**
2 **(*Anguilla rostrata*) eel larvae during the year of spawning**

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Abstract

The distribution of the leptocephalus larvae of the European and American eel collected during recent Sargasso Sea surveys, was used to model the larval drift. The drift trajectories of individual larvae were back-calculated to the estimated time of spawning, using current data from two global oceanographic assimilation models. The results of both models give the same overall result; widespread spawning extended in time from December to March. The drift was also calculated forwards for approximately one year. The forward drift modeling showed that most leptocephali remained in the area south of the Subtropical Frontal Zone. One conclusion is that the majority of leptocephali remains trapped and possibly dies in the retention area. A small proportion of leptocephali are entrained into the Gulf Stream system. An implication is that the spawning success may be highly sensitive to oceanographic and climatic factors that alter the dispersion of leptocephali out from the retention area. An alternative interpretation is that the surveys were made too late after the peak spawning period and that the core spawning area was missed.

37 Introduction

38 European eels (*Anguilla anguilla* Linneus) and American eels (*Anguilla rostrata* Lesueur) have been
39 known to spawn in the Sargasso Sea, since small specimens of the leptocephalus larvae of both
40 species were collected there almost a century ago (Schmidt 1912, 1922). More recent collections
41 verified that the spawning areas of both species are located in the southern Sargasso Sea (Schoth and
42 Tesch 1982; Kleckner and McCleave 1988; Munk et al. 2010), and the history of larval collections and
43 the distributions of anguillid leptocephali in the North Atlantic have recently been overviewed (Miller
44 et al. 2015). The recent sampling surveys found that both species appear to spawn south of frontal
45 features that form in winter and spring in the Subtropical Convergence Zone of the Sargasso Sea
46 (Kleckner and McCleave 1988; Munk et al. 2010).

47 After spawning the larvae are carried by the North Atlantic subtropical circulation towards the
48 American and European shores. The duration of this transport is uncertain and estimates range
49 between one and three years, but estimates in favour of long migration duration seem to be more
50 statistically robust than methods estimating shorter durations (Bonhommeau et al. 2010). The
51 evidence for a single, overlapping spawning area is strong (McCleave et al. 1987; Miller et al. 2015),
52 and modern genetic studies indicate that both species form panmictic spawning populations (Palm et
53 al. 2009; Als et al. 2011). However, the Sargasso Sea extends over a vast area and historically eel
54 surveys are few, usually covering just a part of the full distribution range of the leptocephali.

55 The North Atlantic eel populations have experienced a large and persistent decline in
56 recruitment since the mid-1980s (Castonguay et al. 1994; Dekker et al. 2003). The causes are largely
57 unknown: among the suggestions are anthropogenic factors such as loss of continental habitat,
58 overexploitation or an increased burden of parasites and contaminants (Haro et al. 2000; van
59 Ginneken et al. 2009; Kettle et al. 2011; Freese et al. 2016; Sühling et al. 2015 and 2016). Oceanic
60 factors may also impact the larval transport (Friedland et al. 2007; Miller et al. 2009) as well as
61 primary production and food availability in the larval habitat (Knights 2003; Bonhommeau et al.

2008; Miller et al. 2016). To increase the knowledge about the spawning biology of both Atlantic eel species and the present conditions in the spawning area the German Thünen Institute of Fisheries Ecology conducted leptocephalus surveys in the Sargasso Sea in 2011, 2014 and 2015. Together those surveys give a comprehensive mapping of the distribution of eel larvae both in time and space. The data from the 2011 survey have been analysed by Hanel et al. (2014) to compare leptocephali abundance with earlier surveys using similar sampling methods. The 2014 and 2015 data are presented for the first time here.

One purpose of the present study is to use the observed distribution of leptocephali of both species as starting points for back tracking of the drift of the larvae in a Lagrangian model (Christensen et al. 2007). Using the dates and positions of individual leptocephali as initial values, drift trajectories were calculated backwards in time, using daily current velocity data generated by two high resolution oceanographic reanalysis models, in order to find the probable spawning place corresponding to the observed leptocephalus distribution. This type of analysis has not previously been done for eel leptocephali.

Another purpose is to follow the drift of the same eel leptocephali forwards in time, using the same oceanographic circulation models, for approximately one year from the day of capture. Such drift models have previously been described, seeding the model with tracers in a large area of the presumed spawning region (e.g. Kettle and Haines 2006; Bonhommeau et al. 2009a; Pacariz et al. 2013; Melià et al. 2013; Baltazar-Soares et al. 2014). Similarly, the drift of *Anguilla japonica* and *Anguilla rostrata* larvae has been modelled (e.g. Kimura et al. 1999; Rypina et al. 2014; Chang et al. 2015). What is new in this study is that the initial values are the observed occurrences of larvae and that the starting positions are given a weight proportional to the abundance of leptocephali observed in that point. In this way, the success rate of the forward modelling becomes more representative of a real situation. Both reanalysis ocean models have been used in larval drift modelling earlier (e.g. Melià et al. 2013; Putman et al. 2016). The purpose of using both reanalysis models in parallel and

87 comparing the current fields of the models to the ADCP observations is to get an estimate of how
88 well the models represent reality.

89 **Methods**

90 The surveys in 2011 and 2014 were solely dedicated to eel research and were carried out on the R/V
91 “Walther Herwig III”, a 64.5 m stern trawler. In 2015, an interdisciplinary research expedition
92 studying the ecology of the Sargasso Sea was conducted on board the 94.8 m R/V “Maria S. Merian”.
93 On all cruises *Anguilla* and other leptocephali were collected using an Isaacs-Kidd Midwater Trawl
94 (IKMT) with a 6.2 m² mouth opening, a length of 10 m, and 0.5 mm mesh (<http://www.hydrobios.de>).
95 At most stations, a single, double oblique tow was made between the surface and 300 m depth. In
96 few cases (two stations in 2011 and two in 2014), a second double oblique haul was made to 300 or
97 150 m. The filtered volume was measured and varied slightly due to weather and subsurface
98 currents. Figure 1 shows the station grids of the surveys and Table 1 gives a summary of the sampling
99 period, filtered volume and the total number of *Anguilla* leptocephali belonging to the cohort of the
100 survey year according to species.

101 All catches were sorted on board and all eel leptocephali were tentatively identified according
102 to Böhlke (1989). Total length (TL) was measured to the nearest mm and the larvae were either
103 preserved in ethanol or frozen. All anguillid leptocephali were later identified to a final species
104 designation by analyzing their cytochrome b sequences (Trautner 2013) and 18S rDNA RFLPs
105 following the protocol of Frankowski and Bastrop (2010) with some modifications regarding the
106 restriction enzymes as described in Prigge et al. (2013).

107 At all IKMT stations, a CTD cast was made to a depth of at least 300 m using a SeaBird 911 plus
108 CTD (<http://www.seabird.com>). During the 2015 survey, two hull mounted RDI ADCPs, one operating
109 at 75 kHz and one at 38 kHz (<http://www.rdinstruments.com>), were run continuously during the
110 whole cruise. Data were stored as 10 minute mean values, vertically averaged into 100 depth bins,

each spanning 8 m, centred at depths between 18 and 810 m. The ADCP data were analyzed using a software package developed at GEOMAR Helmholtz Centre for Ocean Research Kiel.

The ADCP data were compared to data from each of the two global circulation models, described below, which were used for the modelling of leptocephali drift. ADCP data from depth bins centred at 50 m and 154 m were compared to model data at the 50/55 m and 150/155 m depth levels. The oblique hauls used in the three surveys gave no information about vertical distribution of leptocephali; instead information about depth distribution was taken from published data by Schoth and Tesch (1982 and 1984) and by Castonguay and McCleave (1987). Both studies concluded that leptocephali <5 mm TL were found over a large depth interval and that there was no difference between day and night. Larger leptocephali show a regular diurnal vertical migration (DVM) with the vertical amplitude gradually increasing with size. As an average for the TL interval 5-25 mm, which is modeled here, approximately 50 m and 150 m was chosen as nighttime and daytime depth respectively. The leptocephali were assumed to spend equal time at both levels. Drift was also modeled with the larvae remaining constantly at the nighttime or daytime depth.

The data from the 75 kHz ADCP were acquired during the periods when the vessel was at a station and moving with a maximum speed of 3 knots. Further, we averaged the ADCP data available at each station for each specific calendar day to generate current velocity values that correspond to grid points and time steps of the model data. Since the time spent at each station varied, the amount of available ADCP data also varied among stations. The model data points were selected based on the minimum distance from the locations of ADCP data collection. Comparison of the two circulation models was performed at the points used for the comparisons with ADCP.

During the cruises and the subsequent analysis, daily maps of Sea Surface Temperature (SST) were used to analyze the position of the Subtropical Convergence Frontal Zone (SCFZ). The front considered to form the northern limit of spawning (Kleckner and McCleave 1988) was taken as the geographical location of the surface expression of the 22.5°C isotherm (as in Friedland et al. 2007).

SST maps produced by the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system were downloaded from the Group for High Resolution Sea Surface Temperature (<https://www.ghrsst.org/>). The datasets contain processed L4 data, gridded at a spatial resolution of $1/20^\circ$. Latitudinal position of the isotherm was determined as the southernmost point at which the SST was equal to or below 22.5°C for each longitude.

Modelling

The total body length of the leptocephali classified as being hatched during the same spawning season as the survey ranged between 5.5 and 26.4 mm for 447 *A. anguilla* and 7.4 to 27.7 mm for 214 *A. rostrata*. In addition, there were 10 leptocephali larger than 39 mm, judged to be “tramps” from an earlier spawning season and not used for the regression or modelling. A linear regression of length as a function of day of the year was derived for all *A. anguilla* leptocephali less than 30 mm TL and the slope was used as a proxy for growth rate. The growth rates were used to estimate the time of spawning of each leptocephalus by extrapolating back to the date when each egg was fertilized.

Only limited data is available on hatching and early growth of *A. anguilla* leptocephali. As part of the PROEEL project (Davidsen 2012), as well as during eel reproduction experiments at the Thünen Institute (pers. comm. Lasse Marohn), eggs were successfully fertilized and studied during the first 6–7 days of the yolk-sac stage. The time to hatching was approximately 48 hours at 20°C and the size of the newly hatched larvae was approximately 3 mm. The size of the larvae doubled during the 6 days post hatching.

Using the regression for the corresponding year, the date of fertilization was calculated for all *A. anguilla* leptocephali in the dataset. If the total length was 6 mm or less, the fertilization date was taken as 8 days before the date of capture. For larger individuals the number of days to grow from 6 mm to the observed size was added to those 8 days and the fertilization date was found by subtracting from the capture date. A similar calculation based on the observed growth rate for the *A.*

rostrata leptocephali was not done. Instead the average growth rate calculated by Tesch (1998) and Boëtius and Harding (1985) was used.

To trace the drift of the leptocephali in time, we used daily output from two ocean reanalysis/synthesis models. The HYbrid Coordinate Ocean Model (HYCOM) model (www.hycom.org) is a general circulation model with isopycnic vertical coordinates, combined with constant level coordinates in the surface mixed layer. We used daily output from the GLBu0.08 version, where native HYCOM data have been interpolated to a uniform 0.08° latitude/longitude grid and 40 standard depth levels. The other model was the Operational Mercator Global Ocean analysis and forecast system (GLOBAL_ANALYSIS_FORECAST_PHYS_001_002, available at www.marine.copernicus.eu), referred to here as the Copernicus model. This model has a 0.08° latitude/longitude grid and 50 vertical levels. The vertical grid is refined at the surface with a denser distribution of layers between 0 and 200 m depth.

Both models assimilate satellite data of sea level anomaly and sea surface temperature (SST) as well as in-situ profiles of temperature and salinity. The models do however differ in several respects. The way they handle the vertical mixing differs and the atmospheric fields forcing of the Copernicus ocean model is taken from the ECMWF (European Centre for Medium-Range Weather Forecasts) Integrated Forecast System while a new atmospheric forecast model, the NAVy Global Environmental Model (NAVGEN) developed by the Naval Research Laboratory (NRL), is used for the HYCOM model. Detailed descriptions of the HYCOM model can be found at <https://hycom.org/hycom/documentation> and of the Copernicus model at <http://marine.copernicus.eu/documents/PUM/CMEMS-GLO-PUM-001-024.pdf>.

Velocity fields from the HYCOM and Copernicus models were used as input in a simple Lagrangian model implemented in Matlab (<https://se.mathworks.com/products/matlab>) to calculate passive drift. Daily velocity grids covering 1st of December 2013 to 30th April 2016 were downloaded and backtracking simulation was done by assigning negative displacement to each particle. Thus,

trajectories of the leptocephali will be going backwards from catch position to the fertilization position. One particle for each collected leptocephalus was seeded at the corresponding catch position and catch date. TL and growth rate was used to calculate the total tracking time for each particle. In the forward tracking a positive displacement is added in each time step, starting in the catch position on the catch date, proceeding until the 30th of April the following year. A time step of 2 hours was chosen and the current vector grid of the oceanographic model was linearly interpolated both in time and space, into the position of the particle at each time step. The value of the time step ensures that the distance travelled is smaller than the grid size for all velocities given by the models, fulfilling the Courant-Friedrichs-Lewy (CFL) stability criterion (Lax and Richtmyer 1956).

Results

Length versus date

The total body length of *A. anguilla* leptocephali as a function of day of the year (Julian date) is shown in Figure 2. The linear regression was calculated for each year separately and for the combined dataset (Table 2). The overall growth rate for the 40 day period was found to be 0.18 mm day⁻¹, which is close to earlier estimates; Boëtius and Harding (1985) arrived at 0.177 mm day⁻¹ and Tesch (1998) at 0.15 mm day⁻¹. An analysis of approximately 14,000 *A. anguilla* leptocephali belonging to the year class of the spawning year in the ICES historic database (Miller et al. 2015) gave a linear growth rate of 0.14 mm day⁻¹ (Righton et al. 2016).

The analysis of the smaller dataset of *A. rostrata* leptocephali shows a large variation (Table 2 and Figure 3). The growth rates (0.09-0.19 mm day⁻¹, with a negative growth rate recorded in 2014) deviates from what has been reported earlier. Tesch (1998) arrived at 0.22 mm day⁻¹ with an intercept at Julian day 0.9 while Boëtius and Harding (1985) report 0.187 mm day⁻¹.

Figure 4 shows the relative frequency of spawning activity in 5 days time bins. The peak spawning of *A. anguilla* is at day 40, corresponding to February 9th, but the spawning period extends

from December to April. The spawning of *A. rostrata* is more spread out in time and with a slightly earlier peak on February 6th.

Backtracking

The 2014 and 2015 data of the Copernicus model for the 55 and 155 m depth levels were used to calculate the drift between the date of capture and the estimated day of fertilization of the egg for all individual leptocephali. Archived data for the Copernicus model only go back to April 2012, which is why the 2011 survey data could not be used in the modeling of drift. Calculation was made assuming both drift at constant depths at the two levels and DVM with 12 hours at each level each day. The same calculations were made using the HYCOM data for the closest standard depth levels, which were 50 and 150 m.

The drift speed was calculated in two ways; as distance over ground, based on the direct distance between the fertilization position and the capture position, and as the distance along the whole drift trajectory calculated for each individual larva. The vector average of the speed and the directions are shown in Table 3, together with the algebraic average of the speed. The vector average of the speed for all individuals is lower than the algebraic; varying between 1 and 3 cm s⁻¹.

Figure 5 shows the centroid and the standard deviation of the longitude and latitude of the capture and fertilization positions of individual leptocephali, modeled using the DVM assumption. The capture positions are slightly more concentrated than the distribution of fertilization positions, but there is only a small change in the center of the distribution. Maps of the individual trajectories between capture and fertilization positions assuming DVM and based on both circulation models, are given as Supplementary material Figures S1 and S2. Figures S3-S6 shows the distribution of fertilization positions resulting from drift at constant depth levels.

Earlier studies have indicated that the spawning area of the European eel is limited to the north by a thermal front which separates southern Sargasso Sea surface water from colder northerly water masses (Kleckner and McCleave 1988). The front consistently occurs in vicinity of the surface

expression of the 22.5°C isotherm (Miller and McCleave 1994; Friedland et al. 2007). Figure 6 shows the position of the 22.5°C isotherm together with the expected leptocephali fertilization positions and drift vectors calculated from the Lagrangian simulations of drift. The mean and standard deviation of the front position, based on SST data collected at ten day intervals, is shown for the calculated periods of fertilization of the leptocephali captured during the 2014 and 2015 expeditions.

Forward tracking

The drift trajectories starting at the capture positions show that the majority of the leptocephali remained in the area south of the SCFZ a full year after the surveys. Few leptocephali entered the Gulf Stream and there was no clear sign of an eastward transport in the frontal jet, as proposed by Miller et al. (2009) and Munk et al. (2010). Figure 7 and 8 give examples of the trajectories found assuming DVM between the 50 and 150 m depth levels, using data from the Copernicus and HYCOM models respectively. Modelling of the drift at constant depths give essentially similar results (see Supplementary material, Figures S7-S10).

An end position north of 35° N was used as a criterion implying that the leptocephali had successfully reached the Gulf Stream system after one year of drift. Assuming DVM and no mortality only 4% of all leptocephali starting in 2015 were successful based on modelling using the Copernicus current data, while 12% were successful using HYCOM data. The corresponding numbers were 1 and 3% of the total, when starting the drift in 2014. Those leptocephali that reached the Gulf Stream were all found to originate from a distinct, single *Anguilla*-positive station per year (Table 4). The average individual distances between capture position and the calculated position a year later was less than 700 km for both species and oceanographic models. Figure 9 shows the relative frequency of individual distances. The total displacement of the centroid of distribution, measured from the time of capture to one year later, was approximately 300 km in a south-westerly direction for *A. anguilla* for both years and 300-400 km towards south-east for *A. rostrata*.

ADCP data

The west-east (u) and south-north (v) velocity components for each of the 49 stations in 2015 were calculated from the ADCP data as well as from the two numerical circulation models at the presumed approximate night-time and daytime depths. All six datasets were tested for normality using the Shapiro-Wilk test and all (except the v-component of the Copernicus model at 150 m depth) were found to be drawn from a normally distributed population at the 0.05 significance level. The Pearson correlation coefficient was calculated pairwise between ADCP data and model data, as well as between the two numerical models. The result shows that in all cases there is a significant correlation, at least at the 0.01 significance level (Table 5).

Deviations between the compared datasets vary substantially from station to station. The average differences in direction between the ADCP and the model datasets range from 54.6° to 65.4° while average magnitude differences range from 0.075 to 0.117 m s⁻¹. In general, the differences found between ADCP data and the model datasets are similar in scale to the differences found between the two models when compared to each other. Figure S11 and S12 in the supplementary material show vector plots of the ADCP and model data.

The HYCOM model data do in general show velocity profiles that vary more with depth than what is shown by the Copernicus model data. The velocity variations are larger both regarding magnitude and direction and are most prominent at shallower depths. The ADCP data show the largest variations shallower than 150 m. The average velocity magnitudes at the shallower depth level are 0.206, 0.115 and 0.217 m s⁻¹ for the ADCP, Copernicus and HYCOM data sets respectively, while average velocity magnitudes at the deeper depth level are 0.147, 0.107 and 0.168 m s⁻¹.

Discussion

Backtracking

Tracing the larval drift back to the expected point of spawning does not show convergence towards a common area. The estimated distribution of spawning places of the leptocephali caught in the surveys was actually wider than the distribution of larvae at the time of the survey. The direction of drift is also highly variable (Figure 6). During 2015, leptocephali caught in the eastern part of the area predominately came from the west while leptocephali caught in the western area came mostly from an easterly direction. In 2014, the drift seems more random. Almost all calculated spawning points are found south of the Subtropical Frontal Zone, as defined by the 22.5°C surface isotherm.

If the assumptions about growth rate and passive drift holds, this means that spawning of both species takes place over a $1-2 \times 10^6 \text{ km}^2$ area and extends over a long period of time. Mortality between the time of fertilization and capture has not been accounted for, but adding natural mortality would not change the picture substantially. The time of spawning should be expected slightly earlier as the number of larger and thus older leptocephali would be underestimated. Introducing mortality may increase the size of the spawning area but not change the position of origin of the leptocephali found in the surveys in a systematic way. The fact that the velocity data from the two models correlate reasonably well with concurrent ADCP measurements, in combination with the fact that both models give similar general results indicating widespread spawning with similar centre of distribution, support the conclusion.

The hypothesis about a linear growth rate based on length can be questioned. Counts of daily rings in the otolith of leptocephali and glass eels show a higher growth rate (Bonhommeau et al. 2010). The one otolith increment study published so far for *A. rostrata* and *A. anguilla* found a growth rate of 0.38 mm day^{-1} (Castonguay 1987). If the growth rate is higher, the calculated date of fertilization would be later in the year and the time for the backtracking shorter. This will not change the general conclusion however. The individual trajectories from the catch positions start the same

but will be shorter. The spawning area would still be larger than the distribution of larvae found in the surveys, without any sign of convergence to a specific spawning area.

There are several uncertainties in the Lagrangian modelling. The oceanographic models used to simulate the drift have uncertainties and the resolution of the current field is approximately 9 km, which will smooth small scale eddies. The magnitude of sub-grid turbulence is unknown and could not been parameterized. If this had been included, the spawning positions of the individual leptocephali should have had an additional uncertainty. The leptocephalus size range found at each station is large, however, and this effect is likely to spread the spawning positions more than the turbulent fluctuations. Another source of uncertainty is the vertical migration of the leptocephali. We have used the available information about DVM, but the empirical data on vertical distribution is not extensive. Since the results from simulations of drift at constant depths do not deviate much from drift with the DVM assumption, this is unlikely to be a major source of error.

A remaining uncertainty is if there is an active horizontal migration of the leptocephali. The typical speed in a direct line between spawning and capture position is approximately 0.05 m s^{-1} (Table 3). With a ratio of direct distance to total trajectory distance of approximately 0.4 this means that the typical drift speed along the trajectories becomes 0.12 m s^{-1} . A 20 mm long leptocephalus has to swim with more than 6 body lengths s^{-1} to overcome that speed. A typical critical swimming speed of adult eels is approximately 1 body length s^{-1} (Quintella et al. 2010) and is probably of the same order of magnitude for a leptocephalus, as the swimming kinematics are similar (Miller 2009). It is thus unlikely that active swimming can substantially alter the size of the spawning area inferred from the modelling. As the speed of displacement calculated for the centroid of the distribution of spawning and catch positions is small, typically 0.01 m s^{-1} , the whole spawning area could have been displaced if enough leptocephali swim actively in the same direction.

The DNA analysis found a small number of hybrids between *A. anguilla* and *A. rostrata*. The calculated position where these were spawned is shown in Figure 6 and is well within the overlapping part of the spawning distributions of the two species.

Forward tracking

The result of the simulation of drift from the capture positions is unexpected. The vast majority of the leptocephali remain more or less in the same area as for an entire year. This is not what would be expected based on estimates of how long it takes for the *A. anguilla* leptocephali to reach Europe. This varies from less than a year based on the count of otolith daily rings (Lecomte-Finiger 1992; Désaunay et al. 2012) to 17 to 28 months based on the estimated number of cohorts present simultaneously in the Atlantic (Miller et al. 2015). Evidently the drift speed implied by the present result is incompatible with the daily ring estimates, and the possibility to reach Europe within two or three years would be very low except for the few individuals reaching the Gulf Stream during the autumn and winter after spawning. As for the backtracking, there may be various explanations. Evident possibilities are the neglect of a possible active, directed migration, where a larger size implies a higher swimming speed (Miller and Tsukamoto In press, this volume) and the uncertainty about the amplitude and depth levels during DVM. Both which are factors that can influence the result of the modeling.

If mortality is taken into account, the result may be realistic however. Mortality will have a large influence over a full year of simulation. The instantaneous mortality of *A. anguilla* leptocephali has been estimated to be approximately 4 y^{-1} (Bonhommeau et al. 2009a). This means for example that of the 406 *A. anguilla* caught 2015 and 2014 only 7 should have survived until April the following year. Actually 8 leptocephali > 38 mm and judged to be “tramps” from an earlier year-class were found in those two surveys. Typical for earlier drift models is also that a very small proportion of the seeded particles make it to the European side. Bonhommeau et al. (2009b) found a success rate of 0.0004-0.0011% for a simulation using DVM. Kettle and Haines (2006) got a much higher, but still low, success rate of 0.7%, accumulated over a range of constant depths in their model.

The scenario suggested by the present modeling is that the area covered by the Sargasso surveys south of the Subtropical Frontal Zone is a strong retention area for leptocephali, reflecting a widespread spawning extended at least over the period January to March. From this area a small flux of leptocephali escapes and is entrained into the Gulf Stream system. The majority of the larvae remains trapped and possibly dies in the retention area. An implication from this is that the leptocephalus migration success, as reflected in the glass eel recruitment in Europe, may be highly sensitive to oceanographic and climatic factors that alter the dispersion of leptocephali out from the retention area. The five- to tenfold difference in the proportion of leptocephali entrained to the Gulf Stream between 2014 and 2015 indicates that the dispersion mechanism may be highly variable.

Another interpretation is that not only does the spawning take place in another time period than what have been used to plan the Sargasso surveys, but the core of the spawning may be somewhere outside the usual survey area covered by Schmidt and all following expeditions. This area should in that case be somewhere adjacent to the presumed Sargasso spawning area but have the property that larvae are transported much more efficient into the fast lane of the Gulf Stream system (or maybe by the counter-current hypothesized by Munk et al. 2010). In this way the surveys could have been too late and in the wrong position to detect the core of the spawning.

Such a hypothesis should explain some of the contradictions in observations of leptocephali:

- The difference between transport duration calculated by daily rings and by drift calculation, the latter assuming a starting point in the usual survey area. C.f. Lecomte-Finiger (1992), Bonhommeau et al. (2010) and others.
- The difference in chemical composition of the leptocephalus otolith core in glass eels sampled in Europe and in the leptocephali caught in the Sargasso (Martin et al. 2010).
- Offer an explanation for the apparent negative evolutionary pressure if spawning takes place in a permanent retention area.

It is unclear where such an alternative core spawning place would be. A possibility is that it is north of the Subtropical Convergence Zone with a faster drift into the eastern part of the Gulf Stream, or further west and south with an injection of larvae into the Caribbean Sea. Both possibilities have been discussed for American eel by Kleckner and McCleave (1982).

Model – ADCP comparison

The comparisons between ADCP and model data show relatively large dissimilarities between all three data sets. Both the Copernicus and the HYCOM circulation models do however seem to generate current data that resembles the measured currents in the sense that there is a general agreement between the directions and the absolute magnitudes of the flow. Due to the low current speeds in the region the relative differences in current speed become quite large, with average magnitudes of the differences being of the order of the average current speeds found within the data sets.

From those comparisons it cannot be concluded that one of the models reproduces the local currents better than the other. At the shallower of the two depth levels, the differences in both direction and magnitude between the HYCOM current data and the ADCP data were slightly smaller than the difference between the Copernicus current data and the ADCP data. At the deeper of the levels, the opposite was true. For both depth levels, the differences between data from each of the two models and the ADCP data were somewhat smaller than the differences between the data from the models when compared to each other.

It should be mentioned however, that most of the time averaged ADCP velocities used for the comparisons were calculated from data collected over rather short time periods, often not spanning over an entire tidal cycle. Tidal induced currents in the Sargasso area are weak. The local semidiurnal tidal amplitude of approximately 0.3 m and a depth of 5000 m result in a maximum current of 0.013 m s^{-1} (Schwidorski 1979). Tidal currents are not included in the oceanographic models so this will to some degree affect the comparison.

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Tables

Table 1. Number of *Anguilla* leptocephali belonging to the cohort of the survey year, and the average filtered volume per double oblique IKMT haul to 300 m.

SURVEY				Leptocephali <30 mm TL			Filtered volume (1000 m ³)	
Year	Stations	Start	End	<i>A. anguilla</i>	<i>A. rostrata</i>	hybrid	Mean	Sdev
2011	52	17-Mar	06-Apr	39	44		62.3	11.3
2014	55	18-Mar	08-Apr	168	53	1	78.0	11.4
2015	49	02-Apr	26-Apr	240	117	2	57.7	15.5

576 Table 2. Linear regression parameters for the total length of leptocephali <30 mm as a function of
 577 Julian date.

Species	Year	slope	intercept	adj R ²	p >F
A. anguilla	2011	0.18	-3.2	0.016	0.0064
	2014	0.15	-1.2	0.046	0.0031
	2015	0.16	-0.9	0.069	2.0E-05
	mean	0.18	-3.3	0.261	0
A. rostrata	2011	0.19	-1.7	0.095	0.0240
	2014	-0.48	57.4	0.026	0.1270
	2015	0.09	7.4	-0.003	0.4180
	mean	0.11	0.1	0.033	0.0039

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580 Table 3. Average straight-line speed and direction between capture position and the calculated
 581 spawning position and the corresponding speed calculated along the trajectory between those
 582 positions based on backtracking calculation using the Copernicus and HYCOM models.

Species	Number	Year	Vertical level (m)	Average speed (cm/s)					
				Copernicus			HYCOM		
				(deg)	start-end	trajectory	(deg)	start-end	trajectory
<i>A ang</i>	240	2015	DVM	236	4.3	11.2	193	7.2	18.6
	168	2014		91	6.3	11.9	128	8.9	17.7
<i>A rost</i>	117	2015		261	2.8	11.1	51	3.8	18.7
	53	2014		147	4.1	14.6	109	4.2	20.1
<i>A ang</i>	240	2015	50	189	5.0	12.7	175	6.0	19.1
	168	2014		137	7.3	14.6	119	10.5	19.7
<i>A rost</i>	117	2015		128	2.9	13.5	96	3.3	19.9
	53	2014		219	4.5	15.4	89	5.1	22.0
<i>A ang</i>	240	2015	150	233	5.0	10.6	232	5.2	16.5
	168	2014		192	6.1	11.4	109	7.4	15.5
<i>A rost</i>	117	2015		188	3.4	11.5	189	4.1	18.4
	53	2014		217	2.9	13.1	201	4.7	17.3

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585 Table 4. Percentage and position of origin for leptocephali that reached north of latitude 35°N after
586 one year of drift.

Year	Model	<i>Anguilla anguilla</i>			<i>Anguilla rostrata</i>		
		%	Long W	Lat N	Long W	Lat N	
2014	HYCOM	1.2	58.0	26.5	-	-	-
2015	HYCOM	12.9	61.0	27.0	11.1	67.0	27.0
2014	Copernicus	1.2	61.0	28.5	7.5	70.0	27.5
2015	Copernicus	5.0	64.0	31.0	0.9	67.0	26.0

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589 Table 5. Correlation of ADCP velocity measurements at 49 stations in 2015 and the simultaneous
590 velocities given by two numerical circulation models.

Pair compared		Velocity component	Night depth		Day depth	
			Pearson r	Sig.	Pearson r	Sig.
ADCP	Copernicus	u	0.433	1.90E-03	0.418	2.81E-03
ADCP	Copernicus	v	0.529	9.47E-05	0.534	7.80E-05
ADCP	HYCOM	u	0.474	5.88E-04	0.456	9.99E-04
ADCP	HYCOM	v	0.485	4.13E-04	0.566	2.24E-05
Copernicus	HYCOM	u	0.400	4.37E-03	0.365	9.98E-03
Copernicus	HYCOM	v	0.506	2.11E-04	0.397	4.72E-03

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Figure captions

Figure 1. Station locations where the IKMT net sampled for leptocephali during the three surveys; 2011 – green, 2014 – blue, 2015 – red. Map produced using Maptitude®.

Figure 2. Individual body lengths of *A. anguilla* leptocephali plotted by the Julian date of collection. Green dots 2011, blue 2014 and red 2015. The year-wise linear regression lines are drawn in the corresponding color.

Figure 3. Individual body lengths of *A. rostrata* leptocephali plotted by the Julian date of collection. Green dots 2011, blue 2014 and red 2015. The year-wise linear regression lines are drawn in the corresponding color.

Figure 4. The distribution of estimated dates of fertilization in 5 day bins, calculated from the observed size distributions and growth rates of the 447 *A. anguilla* in the three surveys. For the 214 *A. rostrata* leptocephali growth rate was taken from literature values. The curves show fitted Gaussian distributions.

Figure 5. The centroids of capture (black) and fertilization positions for the two *Anguilla* species in the years 2015 and 2014, calculated with the Copernicus circulation model data (red) and the HYCOM model (green). The aspect ratio and scaling is the same for all panels, but the latitude and longitude ranges differ between the species.

Figure 6. Vectors connecting the fertilization point and capture positions for the two *Anguilla* species for the years 2015 and 2014, calculated with the Copernicus circulation model data. The red line shows the average position of the 22.5°C isotherm at the surface during the spawning period. The aspect ratio and scaling is the same for all panels but the longitude range differs between the species. Red dots show spawning positions of hybrids.

617 Figure 7. Trajectories of the forward drift of leptocephali calculated using current data from the
618 Copernicus model and DVM between 55 and 155 m depths. All trajectories are for approximately one
619 year of drift, starting at the place and time of capture and ending on 30th April the following year. The
620 trajectories are color coded for 2 month intervals. March-April in the spawning year is in blue, one
621 year later in red. Map drawn using m-maps toolbox for Matlab, developed by R. Pawlowicz.

622 Figure 8. Same as Figure 7 but calculated using current data at 50 and 150 m from the HYCOM model.

623 Figure 9. Relative frequency of individual direct distances, from capture position to the position one
624 year later, in 200 km bins, a) *Anguilla anguilla* and b) *A. rostrata*. Lines and symbols 2014 red, 2015
625 black. Calculation based on drift modeling with daily currents taken from Copernicus data (square
626 symbols) and HYCOM data (circle symbols) and assuming a DVM between 150 and 50 m depth.

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Figures

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677 Figure 9. Relative frequency of individual direct distances, from capture position to the position one
678 year later, in 200 km bins, a) *Anguilla anguilla* and b) *A. rostrata*. Lines and symbols 2014 red, 2015
679 black. Calculation based on drift modeling with daily currents taken from Copernicus data (square
680 symbols) and HYCOM data (circle symbols) and assuming a DVM between 150 and 50 m depth.