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Miller, Michael J.; Westerberg, Håkan; Sparholt, Henrik; Wysujack, Klaus; Sørensen, Sune Riis; Marohn, Lasse; Jacobsen, Magnus Wulf; Freese, Marko; Ayala, Daniel Jiro; Pohlmann, Jan-Dag

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Author for correspondence:

Michael J. Miller

e-mail: michael.miller@nihon-u.ac.jp

[†]These authors contributed equally to this study.

[‡]These authors contributed equally to this study.

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Marine biology

Spawning by the European eel across
2000 km of the Sargasso Sea

Michael J. Miller^{1,†}, Håkan Westerberg^{2,†}, Henrik Sparholt³, Klaus Wysujack⁴,
Sune R. Sørensen³, Lasse Marohn⁴, Magnus W. Jacobsen⁵, Marko Freese⁴,
Daniel J. Ayala³, Jan-Dag Pohlmann⁴, Jon Svendsen³, Shun Watanabe⁶,
Line Andersen⁷, Peter R. Møller⁸, Katsumi Tsukamoto¹, Peter Munk^{3,‡}
and Reinhold Hanel^{4,‡}

¹Department of Marine Science and Resources, Nihon University, Fujisawa 252-0880, Japan

²Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Q1
Stångholmsvägen 2, 17893, Drottningholm, Sweden

³National Institute of Aquatic Resources, Technical University of Denmark, 2800 Lyngby, Denmark

⁴Thünen Institute of Fisheries Ecology, Herwigstr. 31, 27572 Bremerhaven, Germany

⁵National Institute of Aquatic Resources, Technical University of Denmark, 8600 Silkeborg, Denmark

⁶Department of Fisheries, Kindai University, Nara 631-8505, Japan

⁷Department of Bioscience, Aarhus University, 8000 Aarhus C, Denmark

⁸Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen, Denmark

MJM, 0000-0002-4949-6903

It has been known for about a century that European eels have a unique life history that includes offshore spawning in the Sargasso Sea about 5000–7000 km away from their juvenile and adult habitats in Europe and Northern Africa. Recently hatched eel larvae were historically collected during Danish, German and American surveys in specific areas in the southern Sargasso Sea. During a 31 day period of March and April 2014, Danish and German research ships sampled for European eel larvae along 15 alternating transects of stations across the Sargasso Sea. The collection of recently hatched eel larvae (≤ 12 mm) from 70° W and eastward to 50° W showed that the European eel had been spawning across a 2000 km wide region of the North Atlantic Ocean. Historical collections made from 1921 to 2007 showed that small larvae had also previously been collected in this wide longitudinal zone, showing that the spatial extent of spawning has not diminished in recent decades, irrespective of the dramatic decline in recruitment. The use of such a wide spawning area may be related to variations in the onset of the silver eel spawning migration, individual differences in their long-term swimming ability, or aspects of larval drift.

1. Introduction

There is increasing evidence that some marine fishes, sea turtles, seabirds and mammals can make remarkably long migrations to very precise areas for feeding or reproduction [1,2]. Marine fishes such as tunas and sharks can make long migrations [2], and diadromous fishes such as anadromous salmon are famous for their long feeding migrations into the ocean before they return to the exact freshwater streams where each fish was born [3]. However, the catadromous reproductive migrations of semelparous anguillid eels out of fresh and coastal waters into offshore oceans for spawning are unique among migratory species. Anguillid eels have fascinated scientists ever since the European eel, *Anguilla anguilla*, and American eel, *A. rostrata*, and then the Japanese eel, *A. japonica*, were found to migrate long-distances to spawn offshore [4,5]. This was first discovered about a century ago when small larvae, called leptocephali, of the two

64 Atlantic eel species were collected in the Sargasso Sea [4].
 65 These life histories require both the adults to migrate to
 66 their spawning areas and their long-lived leptocephali to
 67 drift in ocean currents to their recruitment areas.

68 The reproductive ecology of anguillid eels has remained
 69 mysterious because spawning areas were only known from
 70 larval catches [4–7] until Japanese eel eggs and spawning-
 71 condition adults were collected recently [8]. Larval catches
 72 of the two Atlantic eel species indicate that they spawn in
 73 partly overlapping areas of the Sargasso Sea and their small
 74 leptocephali are mostly found south of where warm southern
 75 surface water meets cold northern water and fronts are
 76 formed [6,7,9,10].

77 The unique oceanic life history of spawning offshore fol-
 78 lowed by a long larval stage has made it difficult to
 79 understand the causes of recent anguillid eel population
 80 declines, although the possible contributing factors have
 81 been identified [11]. The decline of the European eel is pre-
 82 sently reflected in extremely low glass eel recruitment to
 83 European coastal waters [12] and in lower larval abundances
 84 in the Sargasso Sea [13,14]. Uncertainty about what caused
 85 the declines of the Atlantic eels and the Japanese eel has con-
 86 tributed to them being listed as endangered [15]. This has led
 87 to new oceanographic surveys to study the European eel
 88 spawning area [9,13,16].

89 We use an unprecedented grid of sampling stations to
 90 show that the European eel was spawning across a wide
 91 longitudinal zone of the Sargasso Sea during part of their
 92 2014 spawning season. This was achieved by combining the
 93 collections of larvae made by two oceanographic research
 94 vessels that simultaneously sampled across the entire esti-
 95 mated spawning area. Comparison of our results to an
 96 extensive historical collection database shows that small
 97 larvae were also confined to this same zone during the
 98 same March–April period during past years, which provides
 99 the best estimate so far of the width of the spawning area.

102 2. Material and methods

104 Research cruises of the R/V *Dana* (Denmark) and FR/V *Walther*
 105 *Herwig III* (Germany) collected anguillid leptocephali in 15 alternat-
 106 ing transects of sampling stations occupied moving eastward from
 107 70° W to 49° W from 16 March to 16 April in 2014 (figure 1a).
 108 A 9.6 m² mouth-opening ring net (560 μm mesh; *Dana*) [9] and a
 109 6.2 m² mouth-opening Isaacs-Kidd Midwater Trawl (500 μm
 110 mesh; *Walther Herwig*) [13] were used to collect leptocephali
 111 during both day and night in the upper 300 m. Thus, different
 112 nets and types of flowmeters, and fishing styles were used by the
 113 two surveys (double oblique tows to 300 m depths during *Walther*
 114 *Herwig*, single oblique tows to 200–250 m during *Dana*; electronic
 115 supplementary material) preventing direct abundance compar-
 116 isons. Therefore, presence/absence of larvae was used as evidence
 117 of geographical distribution of spawning. Collected leptocephali
 118 were identified using analyses of their DNA sequences that
 119 consisted of the mitochondrial 16S rRNA gene for species identifi-
 120 cation and 18S rDNA and RFLPs for detecting hybrids following
 121 established protocols [17] (along with some restriction enzymes
 122 modifications [18]) for the *Walther Herwig* specimens, and mito-
 123 chondrial cytochrome b sequences for the *Dana* specimens as
 124 part of a previous study [19]). This enabled unambiguous species
 125 identifications to be made of all European eel larvae, while exclud-
 126 ing any American eel larvae that were also collected in the western
 part of the study area. The spawning area of the American eel
 extends farther to the west than sampling occurred in 2014 [10],

so those data are not included in the present study. Conductivity,
 temperature, depth (CTD) profiles were made at most stations to
 examine hydrography. Catch data from a large database [10] for
 March and April within 75–45° W and 20–32° N were used to
 show the historical distribution of different sizes of leptocephali
 across the spawning area.

3. Results

There were 408 European eel leptocephali collected (29 day
 capture period: 18 March–15 April 2014) by the *Dana* ($N =$
 236, 6.3–26.8 mm, mean \pm s.d.: 12.7 ± 3.3 mm) and *Walther*
Herwig ($N = 172$, 5.5–44.0 mm, 12.9 ± 5.5 mm) surveys
 (electronic supplementary material, figure S1), with no sig-
 nificant differences in larval size between surveys ($p = 0.32$;
 t -test). Larvae ≤ 12 mm were distributed across a longitudi-
 nal range (50–70° W) of about 2000 km (figures 1b and 2a).
 Larvae ≤ 7 and 8 mm were almost as widely distributed
 from west to east across about 1640 and 1480 km, respectively
 (figures 1c and 2a). The latitudinal sampling range and mini-
 mum larval size in each transect varied considerably, but
 small larvae were widely distributed (figures 1b,c and 2c).
 The overall size of larvae increased and the number of
 small larvae decreased in the eastward direction (electronic
 supplementary material, figure S2a) in correspondence with
 the sampling date (electronic supplementary material,
 figure S2b), but small larvae ≤ 12 mm were collected in all
 but the easternmost transect indicating a wide range of
 spawning times and locations. Almost all larvae were
 caught south of the northern front (22°C), but larvae were
 present on both sides of the southern front (24°C) Q3
 (figure 1b; electronic supplementary material, figure S3).

Plots of larval sizes in the historical database for March–
 April in the same region show a strikingly similar pattern in
 both longitude and latitude (figure 2b,d). The only difference
 is that larvae were caught farther south than the transects
 extended in 2014. The longitudinal range of small larvae in
 the database was almost identical to in 2014 except a few
 larvae were collected one degree farther east.

4. Discussion

The collection of ≤ 12 mm European eel leptocephali across
 2000 km of the Sargasso Sea during the two 2014 surveys pro-
 vides the first clear evidence that spawning can occur across
 this expansive region within a short time in one spawning
 season. Larvae ≤ 12 mm were collected from 70–50° W, indi-
 cating widespread spawning several weeks before the
 surveys, because these larvae may be approximately ≤ 20
 days old [20,21]. More recently spawned ≤ 7 and 8 mm
 larvae were almost as widely distributed longitudinally, but
 were less common, possibly because the main spawning
 season was ending as the surveys moved eastward. Within
 this large area of larval distribution, the average growth
 rates of larvae collected by the Danish 2014 survey showed
 no distinguishable spatial trends [21], suggesting all areas
 within the spawning area are equivalent for larval growth.
 Modelling of drift patterns of the larvae collected by the
 German 2014 survey suggested that most larvae are not
 quickly transported very far away from spawning sites [16].
 Therefore, catch patterns in the present study may roughly
 reflect spawning locations.

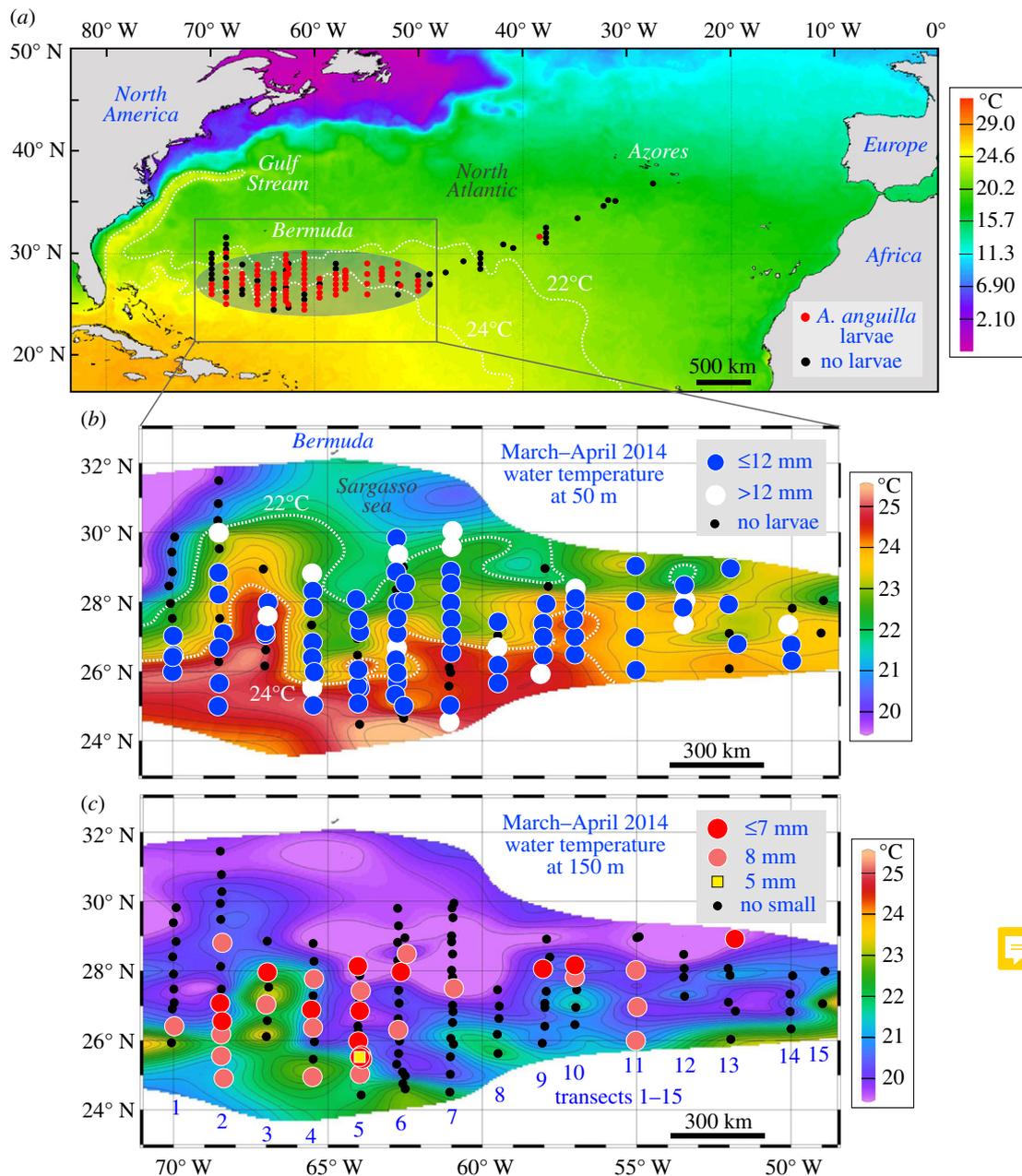


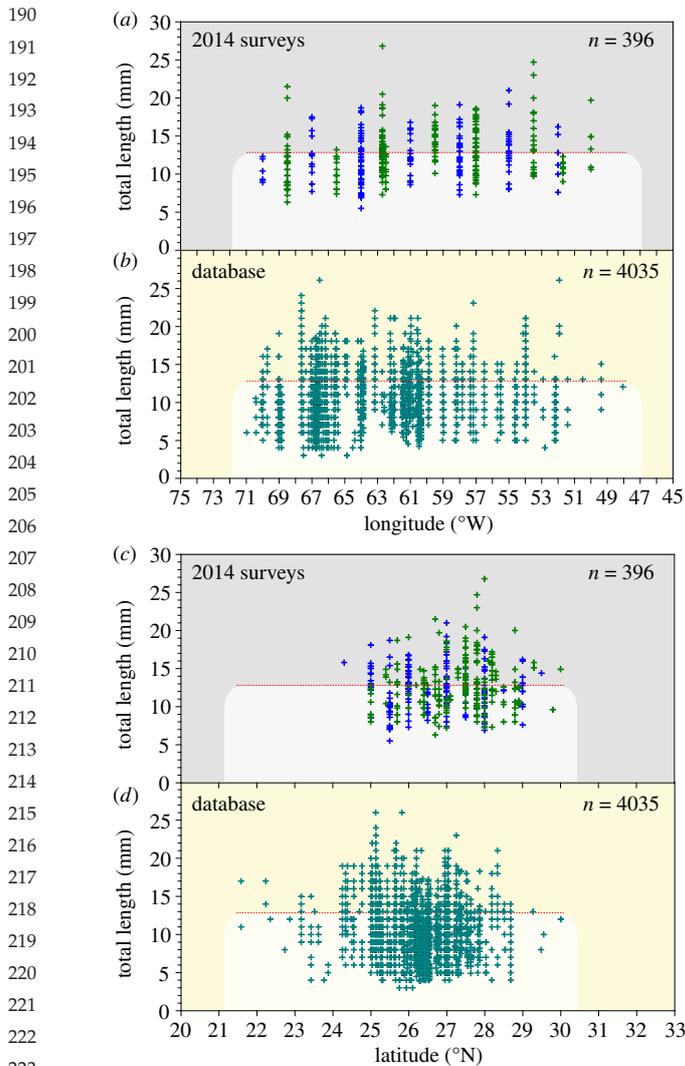
Figure 1. Maps of the 2014 survey showing catch stations of European eel leptocephali (a), catch locations of leptocephali ≤ 12 mm (b), and ≤ 7 , 8, 5 mm (c), in relation to ocean temperature at the surface (a), 50 m (b), and 150 m (c) during the survey. The 22 and 24°C isotherms (white lines in b) are the temperatures associated with fronts. (Online version in colour.)

Data from Schmidt's collections and more recent surveys in the database [10] showed almost the exact same longitudinal distribution-range of ≤ 12 mm larvae. The cruise track of the German 19 March–27 April 1979 survey went in various directions over a wider latitudinal zone during a longer period of time, but also found small larvae over a wide area [6]. Therefore, both historical data and our 2014 collections suggest that the European eel can spawn across at least a 2000 km zone of the Sargasso Sea each year, including in recent years after its population decline while its larval abundances appear to be much lower [13,14].

In comparison, American eels seem to spawn in an overlapping, but narrower longitudinal area in the southwest Sargasso Sea [10], and Japanese eels spawn in an even smaller area west of a seamount ridge [8]. This raises the question of why the panmictic European eel spawns over such a wide longitudinal zone? Studies have been conducted recently to learn about the spawning migrations of European eels by

attaching pop-off satellite-transmitting data storage tags, but so far none of the tracked eels have reached the spawning area [22]. Therefore, where eels from different parts of the European eel continental species range spawn within the wide spawning area is completely unknown.

The possible reasons for spawning over such a wide area may be related to how natural selection has interacted with both the physiological constraints on the long adult migration (approx. 5000–7000 km) and subsequent reproductive success (millions of eggs/female), and the effects of ocean current patterns on larval survival/recruitment success. One factor is that because adult European eels start their spawning migrations out of **freshwater** during many months of each year, it is questionable if all eels can reach all parts of the spawning area during the main spawning season [22]. Eels that migrate early or from areas closer to the North Atlantic and have adequate time and energy might swim to the western side of the spawning area,



Q4 **Figure 2.** Sizes of individual European eel leptocephali collected during the German (blue crosses) and Danish (green crosses) 2014 surveys (a,c), and in the database containing all larvae collected up to 2007 [10] (b,d) in relation to latitude and longitude, highlighting zones of larvae ≤ 12 mm (red line and light shading). (Online version in colour.)

while those that migrate later, from farther away, or have low energy reserves could spawn in the east. Western spawning could increase the probability of larvae entering the rapid Gulf Stream transport across the North Atlantic in the traditionally assumed route into the North Atlantic Drift or Azores Current [10]. The implications of eastern spawning

closer to Europe is unclear regarding the effect on larval transport, even though some eastward larval transport within frontal-jet countercurrents has been hypothesized [9,10]. These flows and eastern spawning might facilitate retention offshore before the larvae move west, or make it easier to reach the western regions of the Azores current if late-stage anguillid larvae can swim directionally to overcome drift, as has been discussed [10,23]. While which if any of these possible factors may have been important cannot presently be determined, strong selection against spawning at either margin seems not to have occurred, which has resulted in an unusually wide spawning area.

Regardless of the reasons for such a wide spawning area, the long migrations of European eels to reproduce across an area as wide as 2000 km represent a remarkable life history that will be better understood as new information emerges about the behaviour and reproductive ecology of these mysterious fishes.

Ethics. There are no conflicts with animal-ethics or conservation policies. The net-based sampling described in the methods is a standard approach for the sampling of plankton and larvae of marine animals.

Data accessibility. The DNA sequences used to identify the European eel leptocephali are deposited in the NCBI GenBank under accession nos. MK483356–MK483528 for the Walther Herwig survey, and sequence data from the previous study that identified the larvae from the Dana survey [19] are deposited in the GenBank under accession nos. KX818059–KX818096, with additional datasets deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v5m24>. Original eel larvae catch-data will be used in future publications by the authors, but requests for access will be considered. Historical collection data of all European eel leptocephali collected up to 2007 that were used to construct figure 2b,d is available online (<http://www.ices.dk/marine-data/data-portals/Pages/Eggs-and-larvae.aspx>).

Authors' contributions. R.H. and P.M. designed and led the research cruises and processing of samples; M.J.M., H.W., P.M. and R.H. analysed catch data and drafted the initial manuscript. All authors participated in the research cruises to collect the European eel larvae, evaluated the manuscript, approved publication, and agree to be accountable for all aspects of the work.

Competing interests. We have no competing interests.

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