

Behavioural variability in the vertical and horizontal oceanic migrations of silver American eels

Mélanie Béguer-Pon^{1,2,*}, Shiliang Shan², Martin Castonguay³, Julian J. Dodson¹

¹Département de Biologie, Université Laval, Pavillon Vachon, 1045 Avenue de la Médecine, Université Laval, Québec, Québec G1V 0A6, Canada

²Department of Oceanography, Dalhousie University, 1355 Oxford Street, PO Box 15000, Halifax, Nova Scotia B3H 4R2, Canada

³Institut Maurice-Lamontagne, Pêches et Océans Canada, 850 Route de la Mer, CP 1000, Mont-Joli, Québec G5H 3Z4, Canada

ABSTRACT: The oceanic spawning migration of American eels *Anguilla rostrata* has remained a complete mystery until the first direct observations were provided by recent tracking experiments. Here we increased the number of observations to better document the variability of migration patterns. Trajectories of 17 eels equipped with satellite tags and tracked for 14 to 58 d over an approximate distance of 630 to 2750 km were reconstructed. Thirteen eels were tracked beyond the continental shelf, including 5 eels into the Sargasso Sea. Similar trajectories were found among the tagged eels: they swam against currents towards the eastern part of the spawning area. Estimated net migration speeds in the open ocean ranged from 34.8 to 54.2 km d⁻¹. In coastal waters, 2 vertical behaviours were observed: (1) repeated up and down movements without a circadian pattern within the first 50 m of the water column and (2) diel vertical migration, with eels swimming to greater depths during daytime (down to 974 m). Eels tracked in the Sargasso Sea all exhibited diel vertical migrations. Eels exhibited significantly greater swimming activity at night, the function of which remains unknown. The daytime and nighttime migration depths varied significantly among individuals and could not be explained by any of the physical factors examined. Some eels appeared to track particular isotherms. Eels tracked in the Sargasso Sea in 2014 ascended to depths shallower than 100 m at night, while eels tracked in 2015 were deeper.

KEY WORDS: *Anguilla rostrata* · Anguillids · Spawning migration · Sargasso Sea · Satellite telemetry · Vertical behaviour

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Anguillid eels are facultative catadromous fish which undertake remarkable long-distance migrations from continental waters to offshore spawning areas at the onset of their maturation (Tesch 2003, Aoyama 2009). The spawning migrations of American and European eels have remained a complete mystery since their spawning grounds were first inferred in the Sargasso Sea over a century ago. However, the recent development of pop-up satellite archival tags (first used by Jellyman & Tsukamoto 2002 to track eels) permits for the first time observations of eels swimming in the open ocean. American eels *Anguilla*

rostrata must migrate distances up to 4000 km (depending on their departure location in continental waters) to reach their spawning site located in the Sargasso Sea. The spawning site was inferred from the collection of leptocephalus larvae over a century ago, and the most probable spawning site according to empirical distribution data for the smallest larvae is estimated to be located in the southwestern part of the Sargasso Sea, around 25.5° N, 72° W (Kleckner & McCleave 1985, Miller et al. 2015). According to the temporal distribution of larvae in the spawning area and back-calculated hatching dates from otolith analysis, the spawning season of American eels occurs mainly from February to April but could extend

*Corresponding author: melanie.beguer@gmail.com

to July (Miller et al. 2015, Kuroki et al. 2017). The first attempt to track maturing American eels en route to the Sargasso Sea started in 2011 (Béguer-Pon et al. 2012). That first attempt failed due to a high predation rate encountered before the eels could escape continental waters. However, tracking experiments conducted in subsequent years provided the first behavioural insights into the migration of American eels in the open ocean and illustrated the feasibility of unravelling the mystery about the migration route and associated behaviours using currently available technologies (Béguer-Pon et al. 2015). The first direct evidence of American eels migrating into the Sargasso Sea was provided by an eel tracked for 2400 km from the Canadian coast to the northern limit of the spawning area (Béguer-Pon et al. 2015). That study revealed diel vertical migration (DVM; eels occupying deeper waters during daytime relative to nighttime), although this was not observed along the entire migratory path. DVM has also been reported in other anguillid eels tracked at sea using either pop-up satellite archival tags (PSATs) (European eels *A. anguilla*: Aarestrup et al. 2009, Westerberg et al. 2014, Wysujack et al. 2015, Amilhat et al. 2016; New Zealand longfin eels *A. dieffenbachii*: Jellyman & Tsukamoto 2005, 2010; Japanese eels *A. japonica*: Manabe et al. 2011; marbled eels *A. marmorata* and Polynesian long-finned eels *A. megastoma* and *A. obscura*: Schabetsberger et al. 2013, 2015), or acoustic tags (Chow et al. 2015). Similar depth ranges were found among species, with depths recorded between 100 and 400 m at night and between 500 and 800 m during the day. Evidence of eels ascending into waters much shallower than 100 m at night (up to the surface) were also reported, including for American eels tracked by Béguer-Pon et al. (2015).

The rationale for diel vertical migration behaviour and the variability in nighttime swimming depth of eels is not fully understood. DVM is a ubiquitous phenomenon in marine and freshwater pelagic communities (Brierley 2014) and often appears as a facultative process that can be substantially influenced by local conditions, including variations in hydrography (Neilson & Perry 1990). The most likely benefit of migrating to deep waters during the day would be predator avoidance; consequently, the circadian cycle would be the most likely cue for migration (Brierley 2014). The depth that species maintain during daytime might be determined by factors such as light levels, water temperature and density. For eels, the most likely hypothesis is that DVM is a trade-off between predator avoidance during the day and the metabolic requirements of gonad maturation af-

forded by pressure and temperature prevailing in shallower waters (Sébert et al. 2007, Aarestrup et al. 2009, Jellyman & Tsukamoto 2010). European eels tracked in the Mediterranean Sea did not experience any change in temperature despite performing large DVM, suggesting that thermal habitat occupation may be a consequence, rather than a driver, of DVM (Amilhat et al. 2016). According to simulations of migration of American eels in the Atlantic, the DVM range does not substantially affect the timing of arrival, but it does affect energy expenditure because of the temperature experienced at the various depths (Béguer-Pon et al. 2016). This is thus an important behaviour, ubiquitous in fish and zooplankton communities in the ocean, that remains imperfectly understood.

Observations of *Anguilla* eels migrating in the open ocean are still rather sparse (e.g. to date, only 1 *A. rostrata* [Béguer-Pon et al. 2015] and 1 *A. anguilla* [Righton et al. 2016] have been tracked entering the Sargasso Sea), which is problematic considering the precarious status of anguillid eels and the possible impact of changing ocean currents on eel survival (Miller & Tsukamoto 2017). The American eel is listed as Endangered on the IUCN red list (IUCN 2014), and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012) recommended that the species be listed as 'threatened' in Canada. Knowledge regarding its oceanic spawning migration is required to understand the life cycle of this enigmatic species and investigate hypotheses about the decline in population observed over the last 30 yr. The objective of the present study was thus to increase the number of observations of eels migrating into the Sargasso Sea: previously published data (Béguer-Pon et al. 2015) were analysed together with new data to better understand the pattern of both horizontal and vertical migrations. More specifically, we aimed not only to describe the trajectories and patterns of migration, but also to compare between years and to link these with the physical marine environment (temperature and salinity gradients, dissolved oxygen concentration, moon phase).

MATERIALS AND METHODS

Capture and tagging of eels

Tracking data from 2014 were used and additional wild silver eels were tracked in 2015, using the same methods as in Béguer-Pon et al. (2015). Silver eels were identified by colouration criteria (visible lateral

line, fully or partially melanised pectoral fins, dark dorsal colouration and silver or dark ventral colouration; e.g. Okamura et al. 2007) and morphometric measurements (total length, fresh body mass, eye diameter and pectoral fin length; see Béguer-Pon et al. 2014). Eels were kept for several days in large tanks. The largest and heaviest eels were selected for tagging to minimize potential negative effects of the external tags. A total of 29 eels were equipped with PSATs (X-tags from Microwave Telemetry, www.microwavetelemetry.com): 15 eels in 2014 and 14 eels in 2015. The total length (TL) of the tagged eels ranged between 98 and 120 cm (mean \pm SD = 110 ± 6 cm), and their body mass ranged between 2.2 and 3.8 kg (2.9 ± 0.4 kg; Table 1). Considering their size, all tagged eels were assumed to be females (total length >400 mm; Castonguay et al. 1994, Jessop 2010). There were no significant differences in length or mass between the 2 years of release (t -test, both $p > 0.5$). In both years, eels were transported by truck to the tagging and release locations in Nova Scotia, Can-

ada: Blandford (SW Nova Scotia, 44.39° N, 64.03° W, depth of circa 50–80 m) in 2014, and Bay St. Lawrence (Cabot Strait, 47.09° N, 60.23° W, depth of circa 150 m) in 2015, representing aquatic shortcuts of circa 1400 and 880 km, respectively. Translocating eels released directly at the exit or outside the St. Lawrence system was done because of the high predation rate encountered by eels released in the St. Lawrence Estuary during previous experiments (Béguer-Pon et al. 2012, 2015) and also because eels from the St. Lawrence River are the largest over the entire range of the species (Jessop 2010). The tagging procedure (surgery and tag attachment method) is fully described by Béguer-Pon et al. (2012, 2015). In 2015, we used 3 rather than 4 attachment points (in 2014), the monofilament wire was replaced by a braided wire (80 lb), and a swivel was added to permit the tag to twist and reduce pressure on the attachment (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m585p123_supp.pdf). This study was carried out in strict accordance with the recommendations of the

Table 1. Capture, tagging, release and transmitting data for 29 American eels *Anguilla rostrata* fitted with X-tags in fall of 2014 (released off Blandford, Nova Scotia, Canada; published in Béguer-Pon et al. 2015) and 2015 (released off Cabot Strait, NS; new data). GCD: great-circle distance between release and first transmission position. Dates are given as dd/mm/yyyy

Eel ID	X-tag ID	Length (cm)	Weight (kg)	Release date	Scheduled tag release date	Date of first transmission	Time after release (d)	GCD (km)	% data transmitted
15	141113	117	3.7	15/10/2014	15/03/2015	30/10/2014	14.4	174	100
16	141106	110	3.2	15/10/2014	15/01/2015	30/10/2014	14.9	146	100
17	141107	111	2.6	15/10/2014	15/01/2015	31/10/2014	15.2	113	100
18	141108	102	2.4	15/10/2014	15/01/2015	31/10/2014	15.3	602	100
19	141114	106	2.8	15/10/2014	15/03/2015	01/11/2014	16.1	158	100
20	141109	111	3.2	15/10/2014	15/01/2015	05/11/2014	20.9	231	100
21	141116	113	3.5	15/10/2014	15/03/2015	05/11/2014	20.9	194	100
22	141115	104	2.7	15/10/2014	15/03/2015	08/11/2014	23.4	340	100
23	141112	112	2.9	15/10/2014	15/03/2015	01/12/2014	46.7	1275	98
24	141119	106	2.8	16/10/2014	15/03/2015	07/11/2014	21.5	99.8	100
25	141111	98	2.2	16/10/2014	15/01/2015	09/11/2014	23.7	280	100
26	141110	111	2.6	16/10/2014	15/01/2015	19/11/2014	34.1	255	99
27	141118	120	3.0	16/10/2014	15/03/2015	30/11/2014	44.7	375	98
28	141105	113	2.8	16/10/2014	15/01/2015	08/12/2014	52.7	1430	99
–	141117 ^a	106	2.9	16/10/2014	15/03/2015	–	–	–	–
29	152075	119	3.75	15/10/2015	15/01/2016	02/11/2015	17.5	239	100
30	152074	114	3.35	15/10/2015	15/01/2016	02/11/2015	17.5	119	100
31	152080	120	3.4	15/10/2015	15/01/2016	06/11/2015	22.1	133	100
32	152078	107	2.75	15/10/2015	15/01/2016	11/11/2015	26.7	179	68
33	152079	102	2.75	15/10/2015	15/01/2016	14/11/2015	29.4	404	100
34	152084	113	2.7	15/10/2015	15/03/2016	16/11/2015	32.0	520	99
35	152081	105	2.55	15/10/2015	15/03/2016	20/11/2015	35.5	711	99
36	152083	100	2.85	15/10/2015	15/03/2016	21/11/2015	36.9	397	100
37	152086	108	2.7	15/10/2015	15/03/2016	23/11/2015	38.4	775	98
38	152077	120	3.2	15/10/2015	15/01/2016	25/11/2015	41.0	826	100
39	152085	104	2.45	15/10/2015	15/03/2016	04/12/2015	49.4	995	100
40	152076	106	2.7	15/10/2015	15/01/2016	08/12/2015	53.5	1230	99
41	152082	109	3.15	15/10/2015	15/03/2016	14/12/2015	59.6	1320	97
42	152087	119	2.9	15/10/2015	15/03/2016	21/12/2015	66.4	1136	95

^aTag failed to detach/transmit, so no eel ID was assigned

Canadian Council on Animal Care. The protocol was approved by the Animal Care Committee, Laval University (Permit Number 2011101-01) and Maurice-Lamontagne Institute, Fisheries and Oceans Canada (Permit Number 12-6C). All surgery was performed under acetylenol (220 ppm), and all efforts were made to minimize suffering. In both years, tagged eels were released within several hours after tagging and at the same time along with 12 and 16 non-tagged eels, respectively, since swimming in schools can provide fish with a number of behavioural and ecological advantages, such as reduced predation risk or energy saving (e.g. Burgerhout et al. 2013). Eels were transported by boat to be released 10 km offshore.

The X-tags (120 mm in length, 32 mm in diameter and 45 g weight in air) were programmed to collect 12-bit resolution measurements of light, temperature (range: -4 to $+40^{\circ}\text{C}$, 0.23°C accuracy) and pressure (range: 0–1296 m, 0.3–5 m resolution) every 2 min for 3 to 5 mo (Table 1). In case of premature death of the eel, a pop-up procedure was programmed to be initiated after 7 (in 2014) or 4 (in 2015) consecutive days of constant depth readings (± 3 m) with a 15 d delay following deployment. Once at the surface, the X-tags transmit (for approximately 3 wk) a subset of the data (15 min intervals for temperature and depth, minimum and maximum light level with sunrise and sunset estimates) to the Argos low earth orbiting satellite system (www.argos-system.org/).

Reconstructed trajectories

The trajectories reconstructed for eels tracked in 2014 by Béguyer-Pon et al. (2015) were used, and trajectories for eels tracked in 2015 were calculated using the same method. Since PSATS do not provide direct geolocation data (except when at the surface after the release mechanism was triggered), migratory tracks must be estimated using the environmental data recorded by the tags (temperature, depth and light). The daily locations, and hence the migratory paths of eels, were reconstructed using the same method developed and fully described by Béguyer-Pon et al. (2015). The temperatures at specific depths and the eel vertical behaviour were used to infer the daily geolocation. Temperatures recorded by the tags were matched with the operational Mercator global ocean $1/12^{\circ}$ analysis and forecast system that uses Nucleus for European Models of the Ocean (NEMO) 3.1, coupled to the thermodynamic-dynamic Louvain Sea Ice Model 2 (LIM2) (see details in Béguyer-Pon et al. 2015). Possible daily locations were constrained

by searching the modelled temperature field from the ocean circulation model within the range of the mean \pm SD (a minimum SD of 1°C was considered) of observed temperatures at the maximum and minimum depths that were reached by the eel each day. X-tags could not reliably estimate times of sunset and sunrise because eels avoid light during daytime, and the tags' light sensor is not sensitive enough to detect very low light levels. However, longitude ranges were estimated when clear diel vertical migration patterns were observed using the demonstrated relationship between these patterns and sunrise and sunset times (Westerberg et al. 2014, Chow et al. 2015; for details, see Béguyer-Pon et al. 2015). The 30 arc-second GEBCO bathymetry was also used to constrain the locations over the continental shelf.

The surfacing locations of X-tags were estimated using the same method described by Béguyer-Pon et al. (2015), i.e. using the temperature and light data collected at the surface and maximum drifting distance and direction (about 4 d of drift for X-tags released in 2015 vs. 7 d for those in 2014).

Analysis of vertical profiles and physical conditions encountered along the migratory paths

For each eel and each day, several variables characterizing the vertical profiles and associated ocean physical conditions were extracted or calculated. The minimum, maximum and average values of depth and temperature were computed from the raw data, whereas the salinity and current values encountered along the migratory paths were inferred using the median reconstructed paths and the operational Mercator global ocean $1/12^{\circ}$ analysis and forecast system. To test for a possible effect of dissolved oxygen concentration on the eels' migration depth (as has been shown for zooplankton and fish; Bianchi et al. 2013), the conditions of dissolved oxygen encountered during the migratory paths were reconstructed using the Global Ocean Biogeochemistry analysis and weekly forecast produced by Mercator Ocean (Paul et al. 2016). The values were extracted from the weekly mean dissolved oxygen available at 50 levels (ranging from 0 to 5500 m) at a $1/2^{\circ}$ horizontal resolution. Vertical profiles of dissolved oxygen at various locations on the migratory paths for both years were also graphically compared.

The mean proportion of time spent within the first 50 m of the water column (surface layer where the current is significantly different from deeper layers), the number of vertical movements and the range of

vertical movements were also calculated. One vertical movement was defined as an ascent preceding a descent (or vice versa) greater than 6 m (equal to the tag's resolution error). Considering that night and day length were not the same (with night length greater than day length at the time and location of the tracking study), a vertical movement index (VMI) was calculated for each day and each eel using the number of vertical movements performed at night or during the day divided by the night or day length (in hours). The range of vertical movements was calculated from the vertical distance covered during 1 vertical movement. To evaluate differences in activity between night and day, the ranges of vertical movements were calculated for each light period (day or night) and each day. To assess and visualize the variability in vertical movements and potential environmental gradients along the migratory paths, the calculated variables were mapped using a colour gradient. Values and gradients in the mean temperature and salinity conditions encountered were calculated for 3 distinct oceanographic regions: the continental shelf, the open ocean north and west of the Gulf Stream and the Sargasso Sea (including the Gulf Stream). Gradients were calculated using the difference in mean daily values between the first and last days within the corresponding area. These gradient values were summarized into tables.

The mixed layer depth and bottom depth of the permanent thermocline (BPT) were calculated along each reconstructed track beyond the continental shelf in order to assess any potential relationship between these depth features and the daytime and nighttime depth distributions of eels. The mixed layer depth was calculated following the threshold method used by de Boyer Montégut et al. (2004). The threshold method gives the depth at which the temperature profiles change by a predefined amount relative to a surface reference value. The typical threshold value of 0.2°C was chosen in this study. The BPT was calculated by statistically searching for the inflection point of the temperature–depth curve using the `davies.test` function from the R package 'segmented' (R Core Team 2014, Muggeo 2015). For each day, the depth locations of selected values of temperature and salinity were extracted from the ocean predictions from an operational global ocean physics 1/12° analysis and forecast system (PSY4, <http://bulletin.mercator-ocean.fr>) in order to visualize the vertical profiles of temperature and salinity along the eels' paths.

To evaluate the potential effect of moonlight on the depth reached by eels at night, the moon illuminated

fraction was calculated using the function `moonAngle()` from the `oce` package (Kelley 2014), and linear correlations between these values and the minimum and average depth reached at night were searched for. To test for an effect of cloud cover on the eels' swimming depth, 2 datasets were used: (1) daily cloud fraction at a horizontal resolution of 0.1° observed by the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra and Aqua satellite (http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MYDAL2_D_CLD_FR&date=2015-10-18), and (2) hourly cloud fraction at a horizontal resolution of ~0.2° produced by the National Centers for Environmental Prediction (NCEP) Climate Forecast System (CFS) (<https://rda.ucar.edu/datasets/ds094.1/>)

Comparison of oceanographic conditions between 2014 and 2015

The monthly mean temperature, salinity and current speed for October, November and December 2014 and 2015 at 4 depth levels (0, ~200, ~600 and ~1000 m, corresponding to depth levels occupied by eels) were calculated based on the daily PSY4 outputs. The subsurface front of the Gulf Stream was defined as the location of the 15°C isotherm at 200 m (Fuglister & Voorhis 1965). The subsurface front position was then mapped for visual comparison. The differences in time–mean temperature, salinity and current speed were computed for the oceanic area where eels were tracked and were represented on maps. The 3 mo mean sea surface height calculated over the period October to December 2014 and October to December 2015 were mapped to visualize differences in eddies between the 2 years of release.

RESULTS

Tracking success and reconstructed migratory paths

Of the 29 X-tags released, 1 never reported (Table 1). Results from our analyses about the fate of the eels (detailed below) are summarized in Fig. S2 in the Supplement. The tags all reported prematurely, i.e. 31.8 d after their release on average (range: 14.4–66.4 d; Table 1). All tags but 1 reported between 95 and 100% of their recorded data (Table 1). Ten eels were tracked for less than 7 d and only over a few km; their X-tags surfaced close to their respective release locations (Tables 1 & 2, Fig. 1). Trajectories of the re-

Table 2. Summary analyses of the archival data recorded by tags attached to American eels *Anguilla rostrata* for the entire tracking duration (*confirmed predation event). Distance travelled was calculated using the mean reconstructed path. Global heading was measured from the release location. Dives d^{-1} and percentage of time within the upper 50 m are means \pm SD. SS: Scotian Shelf; GBNF: Grand Banks off Newfoundland; CPP: coastal pelagic predator; HF: homeothermic fish; DVM: diel vertical movement

Eel ID	Time active (d)	Distance travelled (km)	Area reached	Global heading	Time at bottom (d)	Predation	Vertical behaviour
30	0.1	5			7.4	CPP?	Remained on bottom
29	0.2	5			6	CPP?	Remained on bottom
16	0.7	41			6.9	CPP?	Reversed DVM
15	0.8	42			6.6	CPP?	Descending
17	0.8	41			7.3	CPP?	Descending
18	1.5*				No	HF	Reversed DVM
31	1.9	89			15.8	CPP?	Remained on bottom
32	3.6	99			23.1	CPP?	Remained on bottom
24	4.9	111			8.1	CPP?	DVM
19	7.0	111			1.8	CPP?	DVM for 2 d
21	13.7	725	SS edge	SW	No		Remained mostly in shallow waters (<30 m)
20	13.8	912	SS edge	SW	No		Reversed and unclear DVM
22	16.1	630	SS edge	SE	No		DVM during first 4 d
25	17.1	740	SS edge	SW	No		Clear DVM during first 3.5 d
33	25.2	1357	SS edge	SW	No		Multiple dives in shallow waters
26	26.9	912	SS edge	SW	No		No DVM, remained in shallow waters
34	27.8	1211	West of GBNF	SE	No		Multiple dives in shallow waters
35	31.3	1619	West of GBNF	SE	No		Multiple dives in shallow waters
36	31.8	1523	SS edge	SE	No		Multiple dives in shallow waters—DVM during last 4 d
27	34.1*				No	HF	DVM at the end, more or less marked
37	34.2	1565	West of GBNF	SE	No		DVM/multiple dives in shallow waters
38	37.1	1957	West of GBNF	SE	No		Multiple dives in shallow waters—DVM
23	39.4	2079	West of GBNF	SE	No		Very clear and marked DVM during last 2 wk
39	45.2	2507	Sargasso Sea	SE	No		DVM
28	45.5	2434	Sargasso Sea	SE	No		Very marked DVM during last 10 d
40	49.7	2272	Sargasso Sea	SE	No		DVM
41	55.5	2750	Sargasso Sea	SE	No		DVM
42	58.2	2700	Sargasso Sea	SE	No		DVM

maintaining 17 eels were reconstructed (Fig. 2, Fig. S3 in the Supplement). The uncertainty around their estimated surfacing location was on average 86 km in latitude (range: 9–288 km) and 48 km in longitude (range: 9–123 km; Table S1 in the Supplement). The uncertainty around the daily reconstructed locations averaged 206 km in latitude (range: 100–309 km) and 360 km in longitude (range: 137–582 km; Table S1). In general, the highest uncertainty around the daily reconstructed location was observed along the shelf break front of the Scotian Shelf, preventing us from evaluating potential bi-directional movements (southwestward or northeastward) at the shelf edge for many eels.

The 17 eels for which trajectories were reconstructed were tracked for 14 to 58 d (mean \pm SD = 33 \pm 14 d) over an approximate distance of 630 to 2750 km (mean = 1641 \pm 726 km); these distances were calculated from the median reconstructed daily locations (Table 2). These 17 eels remained on the

continental shelf for 12 to 29 d (mean = 20 \pm 6.5 d; Table 3). Their net horizontal migration speed from the release site to the edge of the continental shelf ranged between 7 and 54.3 km d^{-1} (mean = 30 \pm 14.8 km d^{-1} , Table 3). Of these 17 eels, 4 released in 2014 over the Scotian Shelf and 1 released in 2015 at Cabot Strait went southwest. The remaining 12 eels went southeast (9 released at Cabot Strait in 2015; Tables 2 & 3, Fig. 2). Thirteen eels were tracked beyond the continental shelf. Four were tracked for less than 4 d beyond the shelf. The remaining 9 eels were tracked for 11 to 43 d in the open ocean (Table 4). Five of the 9 eels spent 14 to 29 d in the open ocean before reaching the Gulf Stream and were then tracked for another 5 to 20 d (14.8 d on average) in the Sargasso Sea (Fig. 2, Table 4). Beyond the Scotian Shelf, eels generally migrated southeastward within the area between 59 and 50°W. Five eels seemed to travel eastward/southeastward along the edge of the continental shelf, up to the tail (southern

Depth (m)		Dives d ⁻¹	% time in upper 50 m	Vertical movement range (m)		Temp. experienced (°C)	
Mean	Max.			Mean \pm SD	Max.	Mean \pm SD	Range
211	217	2	0	77 \pm 115	210	6.4 \pm 0.8	5–12.9
176	188	0	0	178	178	6.2 \pm 1.1	2.2–12.9
30	129	9	79	39 \pm 33	129	11.3 \pm 3.2	5.8–15.4
44	110	7	57	26 \pm 19	81	10.2 \pm 2.8	5.7–16.4
37	124	8	83	35 \pm 28	116	10.9 \pm 2.3	5.8–16.2
23	124	3	90	47 \pm 38	124	12.7 \pm 3.4	5.5–16.4
98	109	3.3 \pm 0.6	10 \pm 27	28 \pm 25	98	3.2 \pm 2.5	1.4–13.2
137	159	3.5 \pm 2.6	13 \pm 33	21 \pm 24	140	5.5 \pm 3	3.7–13.9
87	226	7.8 \pm 3.2	46 \pm 19	40 \pm 37	205	10.2 \pm 3.1	5.2–16
91	215	10.1 \pm 6	21 \pm 24	38 \pm 26	172	9.2 \pm 2.9	4.9–16.5
9	145	11.3 \pm 5	97 \pm 5	22 \pm 23	140	15.1 \pm 1.3	5.7–16.4
11	97	8.8 \pm 3	99 \pm 4	18 \pm 11	94	15.2 \pm 1.1	5.7–16.7
30	242	9.1 \pm 5.6	84 \pm 25	34 \pm 39	204	15.4 \pm 2.7	5.7–18.6
32	194	10.9 \pm 4.4	89 \pm 21	26 \pm 23	188	15.2 \pm 3	5.7–19.9
9	167	6.7 \pm 3	100 \pm 1	21 \pm 16	167	13.3 \pm 1	2–16.2
16	156	12.1 \pm 3.4	99 \pm 1	23 \pm 14	156	14.8 \pm 1.3	5.5–17.9
5	323	6.2 \pm 2.8	99 \pm 4	22 \pm 25	323	12.3 \pm 1	4–18.6
17	135	10.5 \pm 3	99 \pm 3	24 \pm 13	108	12.8 \pm 0.8	9.6–15.4
17	307	8.6 \pm 5.1	94 \pm 14	29 \pm 35	274	13.2 \pm 1.6	3–19.9
50	371	12.1 \pm 6.1	82 \pm 24	50 \pm 81	371	14.6 \pm 2.5	5.7–20.4
55	447	10 \pm 3.2	78 \pm 30	39 \pm 45	387	12.2 \pm 2.6	1.4–17.6
44	473	13.2 \pm 6.4	80 \pm 33	42 \pm 51	387	13.2 \pm 2.5	8.2–20.9
82	511	14.6 \pm 4.0	73 \pm 36	53 \pm 85	511	14.2 \pm 2.6	5.0–20.2
293	716	17.6 \pm 5.1	8 \pm 2	50 \pm 63	441	9.8 \pm 3.6	1.2–21.9
144	699	12.9 \pm 4.2	58 \pm 36	68 \pm 95	678	16.8 \pm 4.2	5.7–25.1
346	974	17.8 \pm 6.9	10 \pm 2	65 \pm 80	516	10.2 \pm 4.4	–0.6–22.7
378	877	17 \pm 6.1	8 \pm 2	58 \pm 73	479	11.1 \pm 4.5	0.3–23.1
326	882	15.9 \pm 4.6	1 \pm 5	58 \pm 77	533	10 \pm 4.3	1.5–22.2

tip) of the Grand Banks of Newfoundland. Four eels appeared to migrate directly southward away from the continental shelf edge, but the uncertainty around the reconstructed location could mask a migratory path closer to the Grand Banks of Newfoundland (except for eels 28 and 38; Fig. 2, Table 4, Fig. S3).

The eel tracked the furthest in 2014 (eel 28; Béguer-Pon et al. 2015) showed a relatively straight southward trajectory in the Sargasso Sea compared to the 4 eels tracked in the Sargasso Sea in 2015. It was also the fastest eel to reach the Gulf Stream: 14 d vs. 23 to 29 d for the 4 eels tracked in 2015. However, its mean daily horizontal net migration speed was within the range of the 4 eels tracked in 2015 (53.9 km d⁻¹, vs. 48.5–54.2 km d⁻¹, respectively; Table 4). These eels crossed the Gulf Stream around longitude 54.3–53.1° W, whereas the eel tracked in 2014 crossed it further to the west (longitude 57.6° W; Fig. 2). The eel tracked the furthest in 2015 (eel 41) turned westward

once the Gulf Stream was crossed and continued migrating southward, along a longitude similar to the eel tracked in 2014 (57.9 and 58.3° W, respectively; Fig. 2, and see Fig. 5). Eels generally swam against the currents along their migratory paths (Fig. 3).

The tracks of the 9 eels that were followed the longest in the open ocean ended between 169 km (average using median estimated surfacing location) and 1470 km north of the northern limit of the spawning site (29.5° N; Miller et al. 2015).

Possible high predation rate over the continental shelf

Two of the eels released in 2014 were preyed upon by homeothermic fish (revealed by a sudden increase in ambient temperature): 1 eel at 1.5 d after release and the other at 34 d after release (see details in Béguer-Pon et al. 2015). No predation event by

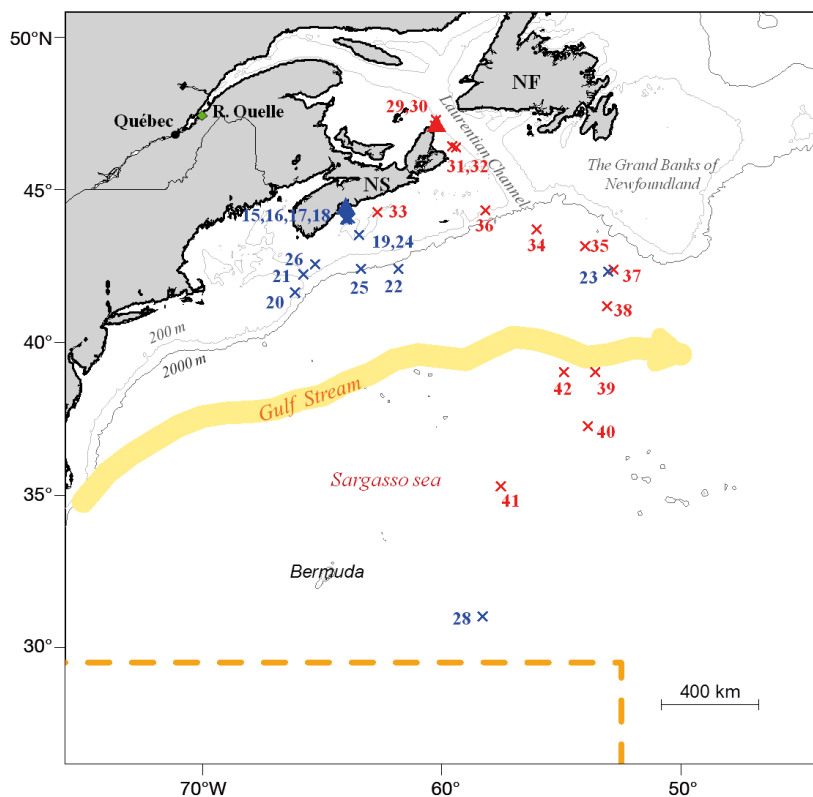


Fig. 1. Release locations (triangles) of American eels *Anguilla rostrata* equipped with satellite tags and estimated surfacing location (crosses). Blue symbols are for eels tracked in 2014 (published in Béguer-Pon et al. 2015); red symbols are eels tracked in 2015. R.Ouelle: Rivière Ouelle (green diamond), the capture location of all eels (brackish estuary) while migrating downstream. NS: Nova Scotia; NF: Newfoundland. Yellow arrow: average location of the North Wall of the Gulf Stream in November; dashed orange line: known limits of the American eel spawning area (see Miller et al. 2015)

homeothermic fish was reported for eels released in 2015. Nine eels (4 released in 2014 and 5 released in 2015) showed an extended period of time on the bottom, from 2 to 23 d (Table 2), shortly following their release. Given the sudden descent to the bottom and the absence of recorded light when the tags were at the bottom, these 9 eels may have been eaten by coastal pelagic predators (or they may have simply been hiding under rocks). The tags rose suddenly to the surface after an extended period at the bottom, either before or after the failsafe period (15 d after release; see an example in Fig. S4 in the Supplement).

Vertical migratory behaviour over the continental shelf and Laurentian Channel

Among the 17 eels that reached at least the continental shelf, 8 exhibited erratic dives in shallow waters (spending 98 % of their time on average within

the upper 50 m of the water column) while the remaining 9 eels performed DVM down to 447 m when migrating in the Laurentian Channel (spending 49 % of their time on average in water deeper than 50 m; Table 3). These 2 different vertical behaviours over the continental shelf were observed in the same proportion (approximately half of the individuals) for eels released in 2014 off Blandford and eels released in 2015 directly in the Laurentian Channel at Cabot Strait. To reach the open ocean, eels released in 2015 had the possibility of using the Laurentian Channel which is deeper than the rest of the continental shelf (maximum depth of 500 vs. 200 m, respectively). At least 5 of the eels released in 2015 did use the Laurentian Channel, exhibiting DVM and reaching depths of 417 ± 34 m, whereas the 5 eels (uncertainty about 2 eels coming from the accuracy of the reconstructed location) that did not use the Laurentian Channel showed erratic dives in shallow waters (Table 3). The eels that migrated in the Laurentian Channel spent less time over the Scotian Shelf than the eels not using the Laurentian Channel (maximum of 18.2 ± 3 d vs. 26 ± 3.5 d, respectively). They also exhibited a higher number of vertical move-

ments, and the number of vertical movements increased along the migratory paths (Table 3, Fig. 4). Eels migrating in the Laurentian Channel experienced lower mean water temperatures than eels migrating on the shelf in shallower waters, and the temperature gradient was generally decreasing in contrast to eels migrating outside the Laurentian Channel (Table 3, Fig. 4). Eels experienced an increasing gradient in salinity (up to 4.4 psu) regardless of their migratory path or their vertical behaviour (Table 3, Fig. 4).

Vertical migratory behaviour in the open ocean

Among the 9 eels tracked more than 4 d in the open ocean, all individuals but 1 (eel 35) exhibited DVM. The maximum depth recorded during DVM was 974 m (eel 40; Table 4, Fig. 5). For all vertically migrating eels except 1 (eel 42), the number of daily vertical movements was higher in the open ocean

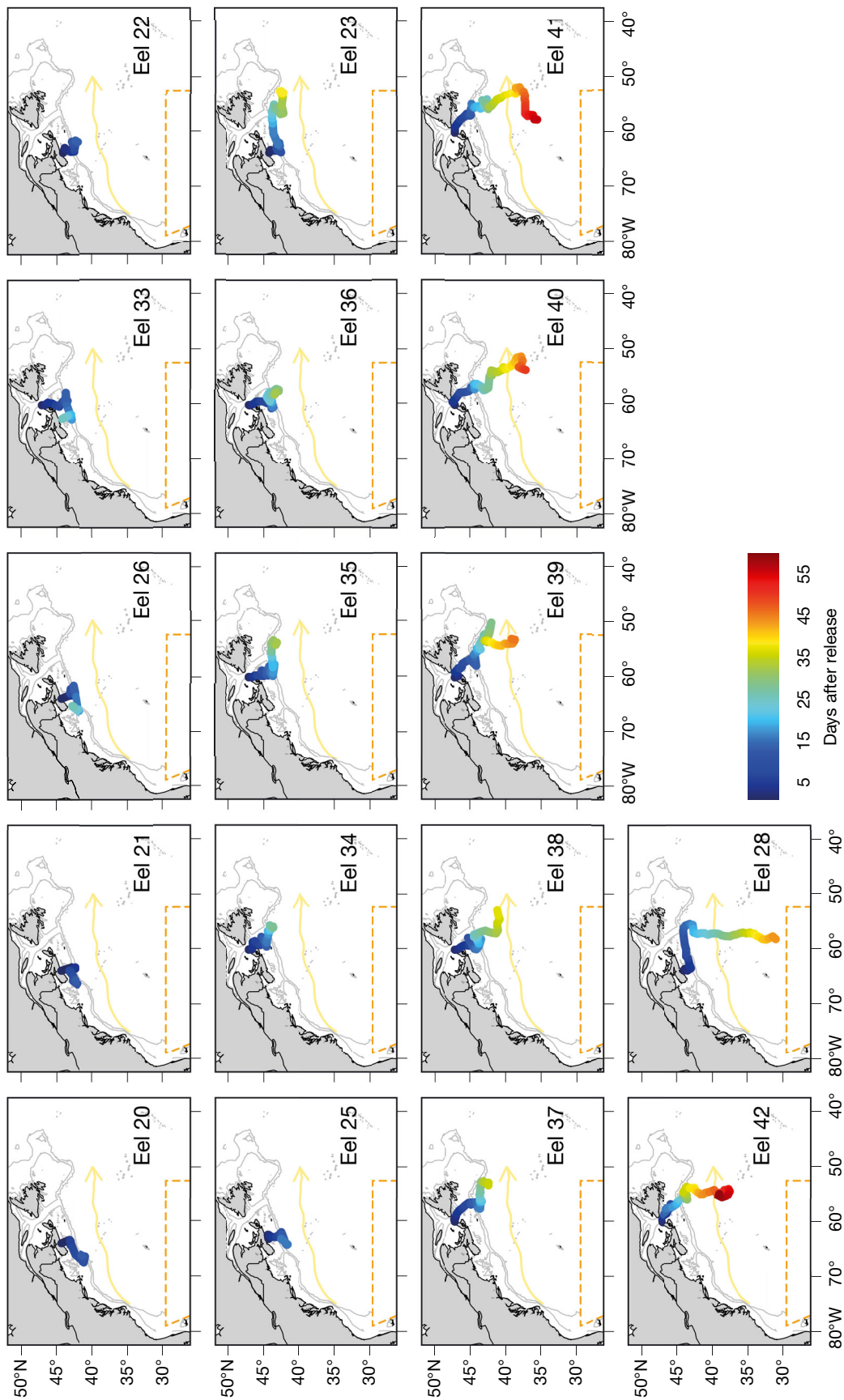


Fig. 2. Median trajectories from the reconstructed daily locations of American eels *Anguilla rostrata* tracked at least up to the edge of the continental shelf. Colour gradient shows the temporal dimension of reconstructed trajectories (each day is represented by a colour). For each day, the median longitudes and latitudes were calculated from all possible locations: although uncertainty was between 100 and 309 km for latitude and between 137 and 582 km for longitude, for clarity it has been constrained here to 100 km. The average accuracy of the reconstructed location is presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/m585p123_supp.pdf. Yellow arrow: average location of the North Wall of the Gulf Stream in November; dashed orange line: known limits of the American eel spawning area (see Miller et al. 2015)

Table 3. Summary analyses of the archival data recorded by the tags attached to American eels *Anguilla rostrata* while migrating over the continental shelf. Global heading was calculated from the release location. Migration speed (min.–max.) was calculated as horizontal net migration speed to reach the Scotian Shelf (SS) edge. Percentage of time within upper 50 m, temperature and salinity gradients (max. depth vs. min. depth), and current speed data are means; LC: Laurentian Channel

Eel ID	Global heading	Period over SS (d)	Migration speed (km d ⁻¹)	Use of LC	Vertical behaviour	Max. depth (m)	Vertical movements per day	% time in upper 50 m	Temp. gradient (°C)	Salinity gradient	Current speed (m s ⁻¹)	Max. depth	Min. depth
20	SW	12	15.8–54.3	–	Erratic dives	97	25.6 ± 11.0	99	2.0	1.0	0.05	0.09	
21	SW	12	15.8–54.3	–	Erratic dives	145	25.4 ± 13.3	97	2.6	2.5	0.11	0.17	
22	SE	13	14.6–34.5	–	DVM	242	20.6 ± 10.4	82	7.8	2.4	0.13	0.15	
23	SE	21	9.0–54.3	–	DVM	151	30.8 ± 9.6	94	4.7	1.0	0.11	0.14	
25	SW	18	10.6–29.2	–	DVM	194	26.2 ± 11.0	89	6.3	2.0	0.21	0.23	
26	SW	27	7.0–38.0	–	Erratic dives	156	28.6 ± 7.9	99	–0.9	0.9	0.10	0.13	
28	SE	13	14.6–47.5	–	DVM	156	26.4 ± 11.9	94	5.1	0.6	0.04	0.11	
33	SW	26	15.4–44.4	No	Erratic dives	167	13.3 ± 6.8	100	1.3	0.4	0.07	0.12	
34	SE	28	14.3–44.4	No	Erratic dives	57	9.1 ± 6.7	100	–0.4	3.2	0.06	0.11	
35	SE	20	20.0–40.0	No	Erratic dives	135	21.2 ± 7.8	100	1.4	2.6	0.07	0.13	
36	SE	29	13.8–44.4	No	Erratic dives	172	15.1 ± 10.2	99	1.3	4.4	0.06	0.12	
37	SE	18	22.2–44.4	Yes	Reversed DVM	447	21.8 ± 7.7	76	4.6	1.6	0.03	0.10	
38	SE	27	14.8–44.4	No	Erratic dives	194	18.1 ± 10.4	99	–2.5	2.4	0.07	0.13	
39	SE	17	30.8–40.0	Yes	DVM	366	27.4 ± 17.4	36	–3.6	3.2	0.04	0.13	
40	SE	20	25.0–36.4	Yes	DVM	447	18.8 ± 8.7	37	–4.5	0.9	0.02	0.09	
41	SE	14	28.6–44.4	Yes	DVM	425	19.6 ± 9.7	40	–2.8	4.4	0.03	0.09	
42	SE	22	18.2–36.4	Yes	DVM	–404	37.3 ± 9.9	6	0.0	4.4	0.02	0.06	

than over the continental shelf (average of 37 ± 4 vs. 26 ± 7 , respectively; Tables 3 & 4). No significant trend (ANOVA, adjusted $r^2 = 0.03$, $p > 0.1$) in the number of daily vertical movements was highlighted once eels were in the open ocean. The 2 eels tracked in the open ocean in 2014 (eels 23 and 28) as well as the 2 eels that had the shortest oceanic track in 2015 (eels 37 and 38) reached very shallow waters, up to the surface, every night, whereas the other eels (all tracked in 2015: eels 39, 40, 41 and 42, longest tracks) swam deeper and deeper along the migratory path without ever approaching the surface (Fig. 5).

All eels tracked in the open ocean swam deeper during the day than at night (see Figs. 5–7, Table 4). Eels tracked in 2015 reached deeper waters than eels tracked in 2014. For instance, the eel tracked the furthest in 2014 (eel 28) swam at a mean depth of 99 ± 54 m at night and 303 ± 265 m during the day, while the one tracked the furthest in 2015 (eel 41) swam at a mean depth of 311 ± 112 m at night and 621 ± 118 m during the day (Fig. 6).

Eels generally swam above the bottom permanent thermocline during both day and night in both years. While the 4 eels tracked over the longest durations in

Table 4. Summary analyses of the archival data recorded by the tags attached to American eels *Anguilla rostrata* while migrating in the open ocean off the continental shelf. Migration speed: mean horizontal net migration speed. Temperature and salinity gradients were calculated from mean values (max. depth vs. min. depth). Current speeds are means. DVM: diel vertical migration; GBNF: Grand Banks off Newfoundland; GS: Gulf Stream; na: not applicable

Eel ID	Reached edge of GBNF	Tracking duration (d)		Migration speed (km d ⁻¹)		Vertical behaviour	Depth (m)		
		Before GS	Sargasso Sea	Median track	Highest–lowest lat.		Max.	Mean Day	Mean Night
23	Yes	20		49.7	21.7	DVM	511	252 ± 201	66 ± 48
28	No	14	19	53.9	45.7	DVM	699	303 ± 265	99 ± 53
35	Yes	13		34.8	19.0	Erratic dives	129	21 ± 16	26 ± 12
37	Yes	18		38.2	19.4	DVM some days	199	52 ± 47	23 ± 11
38	No	11		60.7	39.9	DVM	473	182 ± 134	73 ± 38
39	Yes	29	5	54.2	20.6	DVM	716	502 ± 64	218 ± 72
40	No	24	11	50.0	24.7	DVM	974	621 ± 147	272 ± 97
41	No	23	20	51.7	24.6	DVM	877	621 ± 118	311 ± 112
42	Yes	24	14	48.5	16.7	DVM	882	582 ± 135	248 ± 87

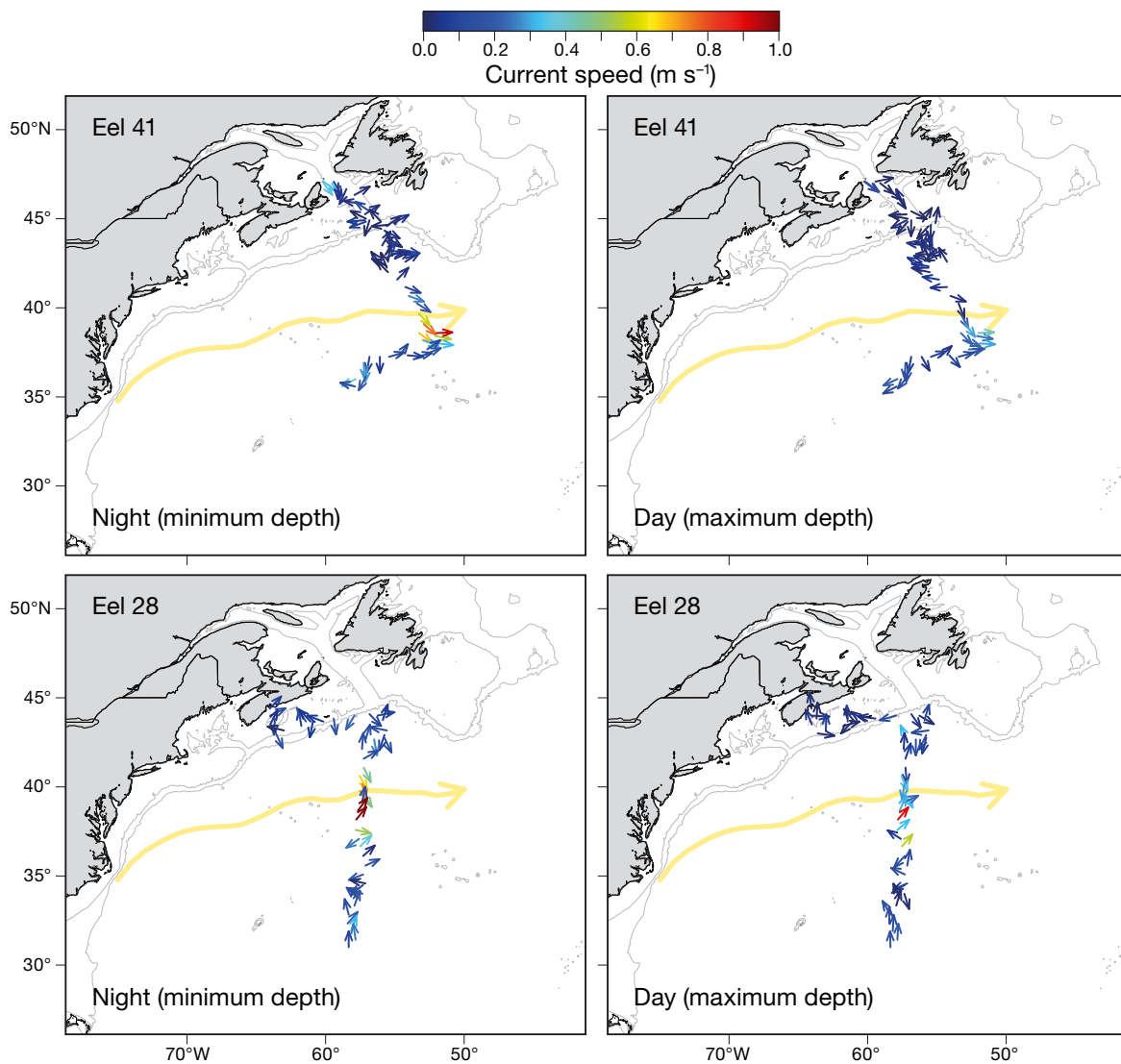


Fig. 3. Mean ocean currents experienced along the median migratory path of American eels *Anguilla rostrata* 41 (tracked in 2015) and 28 (tracked in 2014). Arrows indicate current direction; speed is represented by the colour gradient. Yellow arrow: average location of the North Wall of the Gulf Stream in November

Mean vertical movements d ⁻¹	% time in upper 50 m	Temp. gradient (°C)		Salinity gradient		Current speed (m s ⁻¹)	
		Before GS	Sargasso Sea	Before GS	Sargasso Sea	Day	Night
37.3 ± 10.9	51	5.3	na	2.4	na	0.16	0.31
34.4 ± 6.9	45	5.0	-0.6	3.1	0.1	0.18	0.28
21.7 ± 7.5	93	1.4	na	3.3	na	0.05	0.10
21.6 ± 7.3	83	0.3	na	2.1	na	0.09	0.14
37.1 ± 9.2	36	7.8	na	0.3	na	0.10	0.20
36.9 ± 9.6	3	5.8	0.1	2.0	-0.1	0.08	0.17
42.2 ± 10.5	2	4.9	0.6	3.2	0.0	0.07	0.11
38.5 ± 9.8	0	5.0	1.3	1.2	0.2	0.10	0.18
30.8 ± 8.9	0	5.5	0.1	1.0	0.2	0.05	0.12

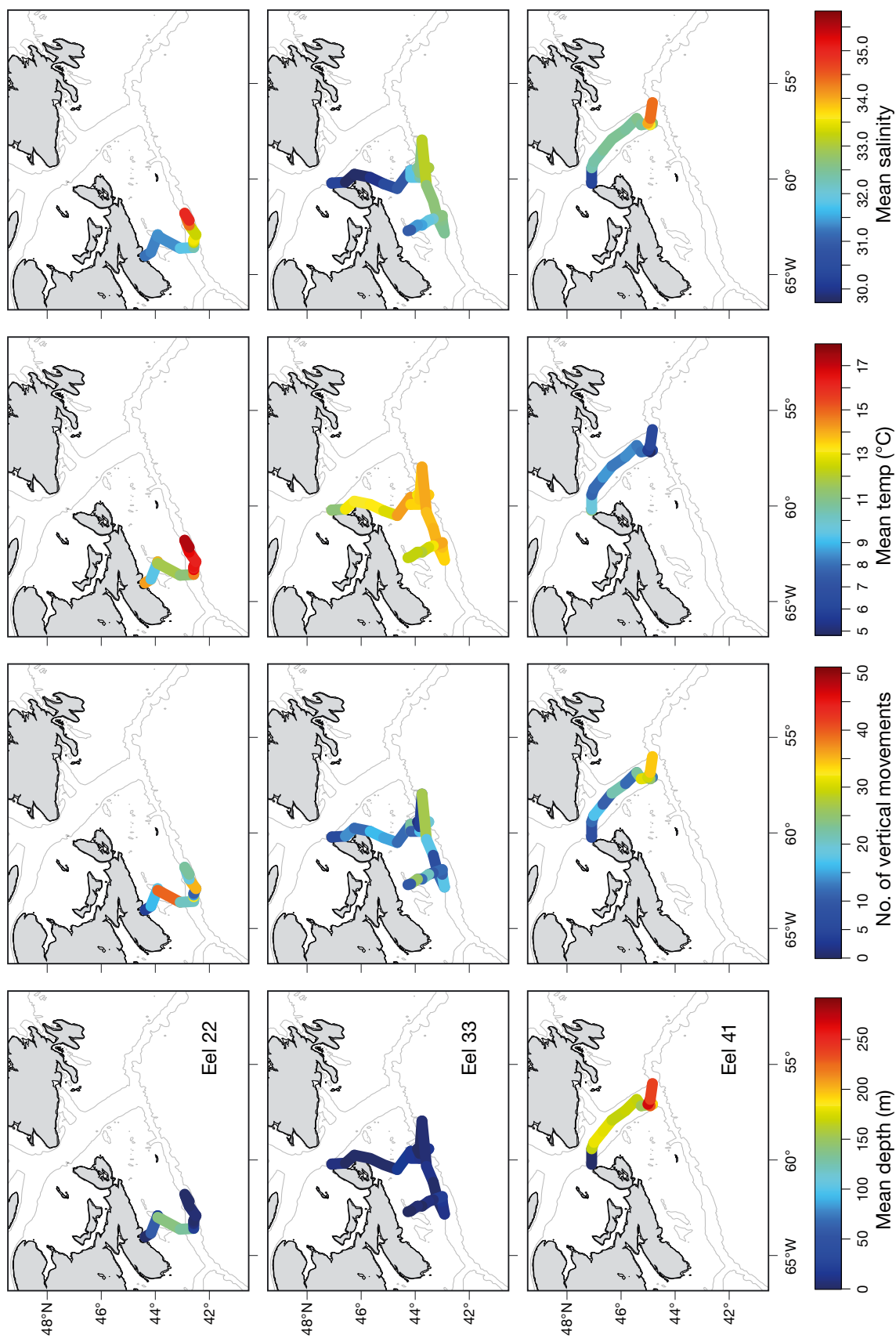


Fig. 4. Diversity in the daily mean physical conditions (depth, temperature, salinity) and number of daily vertical movements along the reconstructed migratory paths over the continental shelf illustrated for 3 American eels *Anguilla rostrata*. Salinity was reconstructed using physical model outputs, whereas temperature was recorded by the satellite tags. Uncertainty around the mean trajectory is not fully represented here (constrained to ~50 km here for clarity)

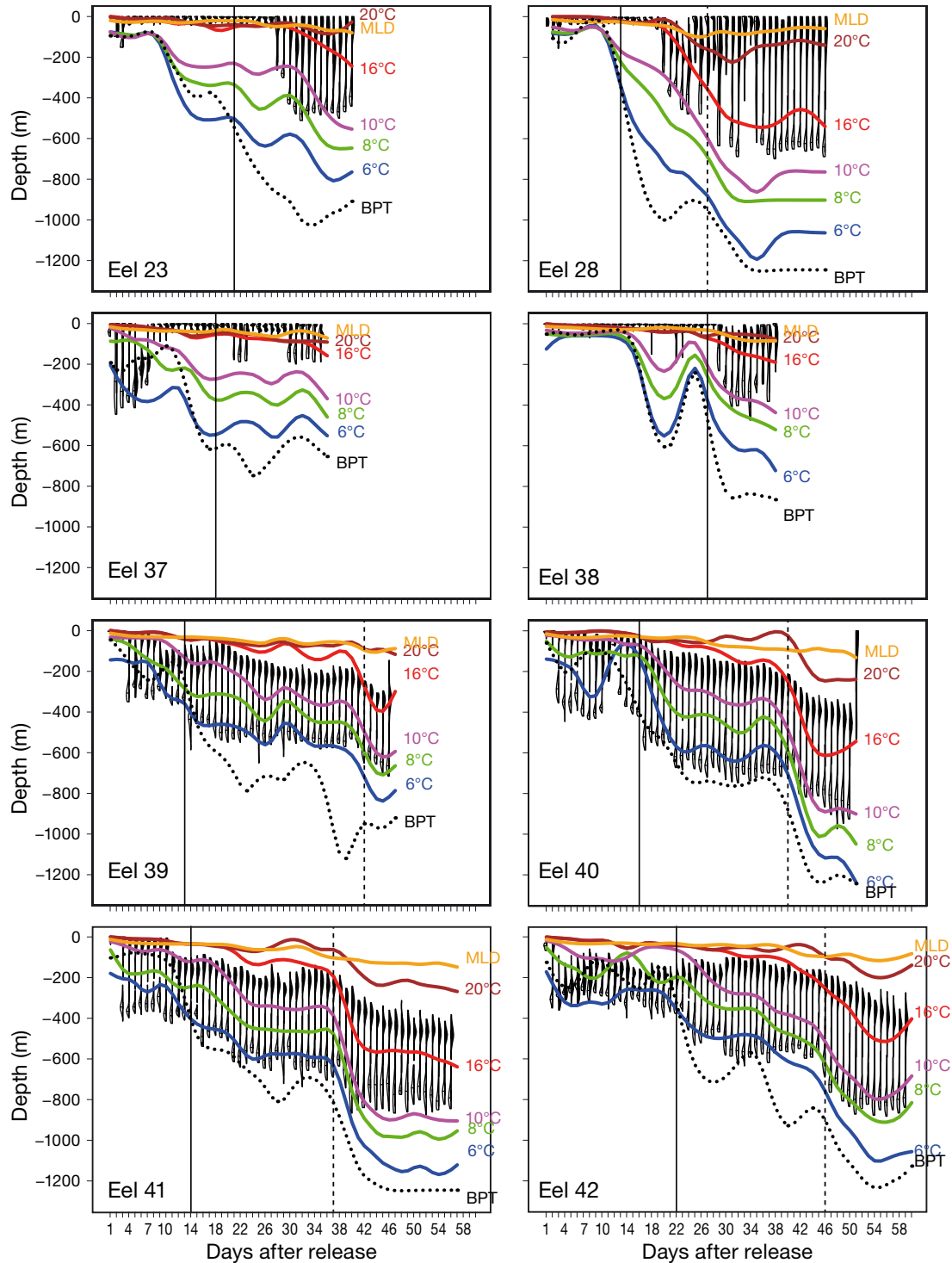


Fig. 5. Depths experienced by American eels *Anguilla rostrata* tracked for the longest durations during their southward migration from the Canadian coast to the Sargasso Sea. Data are shown as violin plots. Black (white) violin symbols indicate the depths occupied at night (day). Maximal and minimal values for each day are indicated by the upper and lower limits of each violin symbol, and the width of the violins shows the kernel density distribution of observations at that value. Colored contour lines indicate the thermal structure of the water column at the reconstructed geolocation (for each day). MLD: mixed layer depth; BPT: bottom depth of the permanent thermocline (at the reconstructed median location). The black vertical line represents the day on which eels crossed the continental shelf (includes the Laurentian Channel), and the dashed vertical line marks the day at which eels crossed the North Wall of the Gulf Stream and entered the Sargasso Sea.

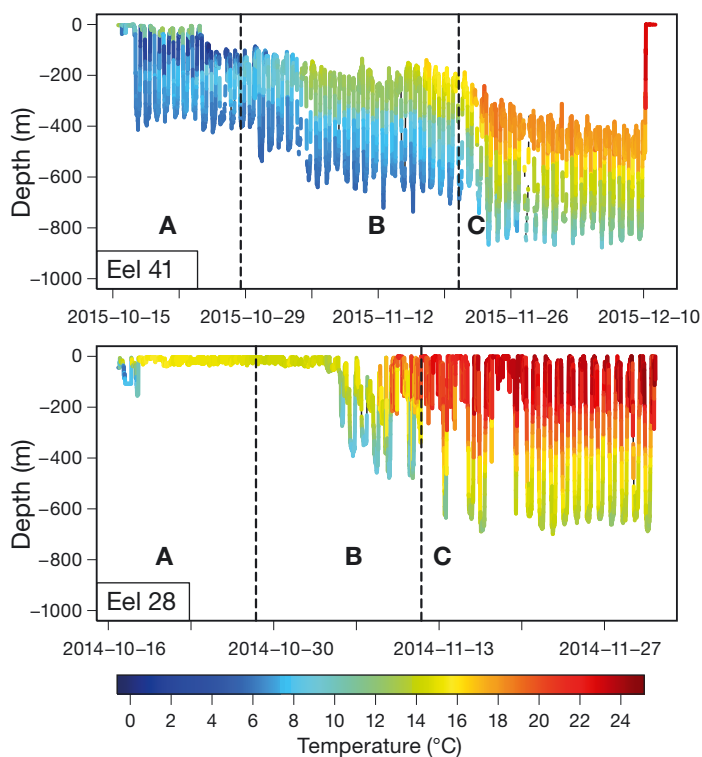


Fig. 6. Vertical profiles of the 2 American eels *Anguilla rostrata* (eels 41 and 28) tracked over the longest durations with temperatures experienced superimposed (raw data). Eel 41 was released in 2015; eel 28 was released in 2014. Area A is over the continental shelf (including the Laurentian Channel), Area B is in the open ocean off the shelf before crossing the Gulf Stream, and Area C is in the Sargasso Sea, including the Gulf Stream

2015 (eels 39–42) swam below the mixed layer depth, the 2 eels tracked in 2014 and the ones tracked for the least time in 2014 swam above or close to the mixed layer depth at night (Fig. 6, Fig. S5 in the Supplement). The 4 eels tracked over the longest durations in 2015 seemed to be tracking isotherms until they crossed the Gulf Stream (Fig. 5, Fig. S5). Indeed, their deep daytime migration depth corresponded to the 6°C isotherm, whereas their shallower nighttime migration depth corresponded to the 16°C isotherm. However, no such relationship was observed for the 2 eels tracked in 2014, as they swam above the 8°C isotherm, nor for the 2 eels tracked for the least time in 2015 (Fig. 5). Eels swimming in shallower waters experienced higher temperatures along their migratory paths. For instance, eel 28 tracked in 2014 experienced an average temperature of $15.3 \pm 3.6^\circ\text{C}$ during the day and $19.1 \pm 3.8^\circ\text{C}$ at night (up to 25.1°C) in the open ocean, while eel 41 tracked in 2015 experienced an average temperature of $8.6 \pm 3.4^\circ\text{C}$ during the day and $14.5 \pm 2.7^\circ\text{C}$ at night (up to 23.1°C ;

Fig. 6). An increasing gradient in the mean temperature and salinity conditions was observed during the migration between the edge of the continental shelf and the north wall of the Gulf Stream: $+4.9$ to $+5.8^\circ\text{C}$ and $+1.0$ to 3.4 PSU, respectively (Table 4). Along their migratory paths in the Sargasso Sea, there was very little or no horizontal gradient in the mean temperature or salinity experienced (-0.6 to 1.3°C and -0.1 to 0.2 PSU, respectively; Fig. 4, Table 4).

No relationship between the eels' migration depths and any isohaline was evident in both years of tracking (Fig. S6 in the Supplement). No relationship between the concentration of dissolved oxygen and the eels' swimming depth was evident (Fig. S7 in the Supplement). Eels which swam in shallower waters experienced higher concentrations of dissolved oxygen. Vertical profiles of dissolved oxygen along the migratory path were similar between 2014 and 2015 at comparable locations and periods (Fig. S7).

No relationship between the moon phase/illumination and the depth eels reached at night (average and minimum) was observed (linear correlation test, $p > 0.1$). The cloud fraction along the reconstructed migratory paths was very high in both years (e.g. 100 % during 84 % of the migratory period of eel 41); therefore, no correlation between this physical factor and the eels' depths was evident.

For all but 2 eels (37 and 38) tracked in the open ocean, a higher activity at night than during the day was observed, i.e. eels explored a greater depth range when swimming at night (205 ± 76 m at night vs. 110 ± 61 m, during the day) associated with a greater number of vertical movements ($\text{VMI}_{\text{Night}} = 0.84 \pm 0.26$, $\text{VMI}_{\text{Day}} = 0.54 \pm 0.23$; Fig. 7). As previously mentioned, eels experienced higher temperatures at night than during the day (for instance average of $14.7 \pm 3.4^\circ\text{C}$ at night and $8.6 \pm 2.8^\circ\text{C}$ during the day for eel 41), due to their shallower location at night (Fig. 7). Despite greater depth amplitude experienced at night (associated with greater number of vertical movements), no significant difference in the variability in temperature experienced during daytime and nighttime was revealed (Wilcoxon rank sum test for each eel, $451 < W < 642$, all $p > 0.05$; Fig. 7). In other words, the vertical temperature gradient experienced at night was similar to the one experienced during the day (Fig. 7).

Characteristics and comparison of oceanic conditions in 2014 and 2015

The subsurface front of the Gulf Stream (location of the 15°C isotherm at 200 m) was not qualitatively dif-

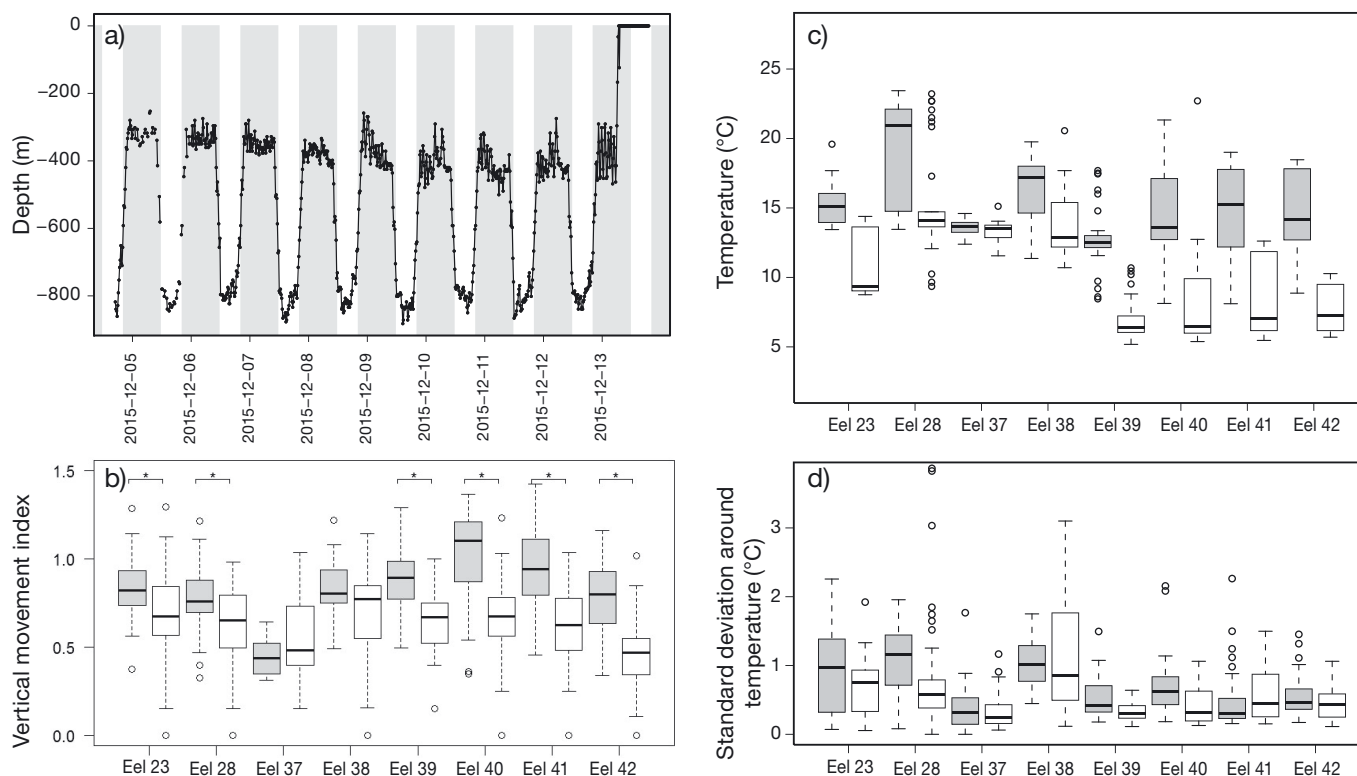


Fig. 7. Differences in the vertical behaviour of American eels *Anguilla rostrata* tracked in the open ocean, according to time of day: (a) vertical profile of eel 42 during its last 9 d of tracking (while in the Sargasso Sea). These raw observed data allow visualizing the higher frequency of vertical movements performed at night (grey areas) relative to daytime (white areas). (b) Vertical movement index calculated for the 8 eels tracked the longest in the open ocean. For all eels except 37 and 38, the vertical activity is higher at night (grey) than during the day (white). ‘**’ indicates a significant difference between night and day (t -test, $p < 0.05$). (c) Temperature experienced at night (grey) and during the day (white) in the open ocean. (d) Absence of significant difference in the temperature gradient experienced at night (grey) and during daytime (white). Boxplot limits — bar: median; box: interquartile range (IQR); whiskers: min./max. values within $1.5 \times \text{IQR}$; dots: outliers

ferent between 2014 and 2015 (October to December; Fig. S8 in the Supplement). The Gulf Stream was stronger in 2015 relative to 2014 (see 0.5 m and 186 m depths; Fig. S9 in the Supplement). Comparing sea surface heights indicated that there were fewer eddies in the Sargasso Sea in 2014 than in 2015 (Fig. S10 in the Supplement). Accordingly, currents experienced by eels in the Sargasso Sea may have been less variable in 2014 than in 2015 (Fig. S9). The Laurentian Channel and adjacent area were also warmer and saltier in 2015 than in 2014 (by $\sim 3^\circ\text{C}$ and ~ 1 psu, Fig. S9).

DISCUSSION

Our study reports unique observations of maturing American silver eels migrating from marine coastal waters into the Sargasso Sea. Migration routes were reconstructed for 17 eels (tracked for 14 to 58 d),

including 13 that were tracked beyond the continental shelf and 5 tracked into the Sargasso Sea for 5 to 20 d. Behavioural variability in their vertical and horizontal ocean migration is highlighted, shedding some light on the spawning migration of eels but also raising questions about their orientation mechanism and the influence of the physical environment.

Reconstructed routes showed relatively similar oceanic trajectories of American silver eels, with a southeastward orientation over and immediately after crossing the continental shelf followed by a relatively abrupt change in direction southwestward. The reconstructed routes obtained in this study, together with results from previous modelling work which simulated the migration of silver American eels from the edge of the shelf off Nova Scotia to the northern limit of the spawning area (Béguer-Pon et al. 2016) allow us to clarify several aspects of the marine migration of eels. It first appears that eels do not orientate directly toward the core spawning

area. The latter (72° W, 25.5° N) is the most probable spawning site according to empirical distribution data of the smallest larvae (Kleckner & McCleave 1988, Miller et al. 2015) and is supported by the modelling work of Rypina et al. (2014, 2016). Instead, eels seem to navigate toward the eastern part of the spawning area. In each year, the longest track (in distance) ended around longitude 58° W and at approximately 170 and 650 km north of the northern limit of the spawning area. While the path of the eel tracked the furthest in 2014 (eel 28) was relatively straight southward, eels tracked the furthest in 2015 frequently changed direction. The more dynamic conditions of the physical environment observed in 2015 (stronger Gulf Stream and larger number of eddies) could explain the greater dispersal of eels tracked in 2015. European eels tracked at sea also showed trajectories that contain meanders that could be related to entrapment within eddies (Righton et al. 2016). Currents may affect the trajectories of eels but, as was suggested in the modelling work of Béguer-Pon et al. (2016), currents are not strong enough to deflect eels from their final destination. True navigation abilities imply the involvement of an inherited bi-dimensional map, such as proposed for Pacific salmon (Putman et al. 2014) and discussed by Béguer-Pon et al. (2015). Once at the northern limit of the spawning area, which corresponds to thermohaline fronts (Kleckner & McCleave 1988), eels could use other orientation cues, such as pheromones that would allow eels to congregate at spawning time (Tesch 2003).

Given the ocean circulation of our study area and based on results from Béguer-Pon et al. (2016), it is clear that eels were mainly swimming against the ocean current (rather than drifting, which could not lead them southward) and at average speeds greater than 0.3 m s⁻¹. The net horizontal migration speeds reported in our study (34.8–54.2 km d⁻¹) are much higher than for the other *Anguilla* spp. tracked at sea (2–51 km d⁻¹ for *A. anguilla*: Aarestrup et al. 2009, Westerberg et al. 2014, Wysujack et al. 2015, Amilhat et al. 2016, Huisman et al. 2016, Righton et al. 2016; 15.1–31.3 km d⁻¹ for *A. dieffenbachii*: Jellyman & Tsukamoto 2002; average of 10 km d⁻¹ for *A. marmorata* and *A. megastoma*: Schabetsberger et al. 2013, 2015). However, ocean currents were not taken into account in those studies, except in Wysujack et al. (2015), who indicated that current speeds and direction were within the range of observed migration speed, making it impossible to distinguish between active and passive movements. The absence of consideration of ocean currents makes comparison of migration speed difficult and the assess-

ment of swimming speeds impossible. Future studies should take ocean currents into account. Field studies that track eels at sea at a finer resolution and that use accelerometers coupled with speedometers are required (only 2 studies of this kind have been conducted so far: Westerberg 1984, Chow et al. 2015). The development and use of modelling work should also be encouraged, even if the actual resolution of reconstructed tracks in combination with the uncertainty in the oceanographic modelling data would hamper accurate estimates of swimming speeds. This parameter is key for estimating energy expenditure and migratory success (Béguer-Pon et al. 2016), and ultimately for investigating hypotheses about the population dynamics of eel species.

Our study revealed a variability in vertical migrations that was not explained by the physical factors examined and that did not seem to affect the eels' ability to orientate toward the spawning area. Two vertical migration patterns were observed over the continental shelf and in the open ocean: (1) repeated up and down movements without a circadian pattern in shallow waters (most of the time spent within the first 50 m of the water column) and (2) DVM, with eels swimming to greater depths during the daytime (down to 974 m) relative to nighttime. Eels exhibited either only 1 of these behaviours or both in any order (for instance starting with DVM for a few days followed by erratic dives or vice versa). The purpose of the erratic dives is unknown. We speculate that it represents exploratory behaviour to detect orientation cues or possibly other eels. Although apparently facultative behaviour over the continental shelf, all eels tracked in the Sargasso Sea (N = 5) exhibited DVM. This behaviour was also observed for other eel species tracked at sea (Jellyman & Tsukamoto 2002, 2005, 2010, Aarestrup et al. 2009, Manabe et al. 2011, Schabetsberger et al. 2013, Amilhat et al. 2016, Righton et al. 2016). Tracking studies showed that the DVM behaviour persists for several months, at least up to 10 mo in the case of European eels (Righton et al. 2016). In general, depths reached by eels were quite similar among species and individuals, i.e. circa 100–400 m at night and 500–800 m during the day, but some variability has been observed. In several studies, including the present one, the daytime migration depth increased as the eels migrated toward their spawning area. Eels could be tracking isolines, i.e. tracking the light extinction point which becomes deeper with the increasingly clear waters further away from the continental shelf, as suggested by Righton et al. (2016). Avoiding light would be a strategy for reducing the predation risk during the day

(Neilson & Perry 1990). One important behaviour observed during our study that has not been reported by previous studies (but nevertheless is evident in their data; e.g. Chow et al. 2015) is the reduced vertical activity of eels during the day (i.e. while in deeper water) which is characterized by a smaller number of vertical movements and a lower range of depths experienced. This reduced vertical daytime activity could reduce the risk of attacks by predators that detect the movements or turbulence generated by their prey (Yamashita et al. 1985). It could also be associated with greater horizontal displacement during the day than at night. The resolution of our data does not allow testing this hypothesis (observations of horizontal movements at the hourly scale are required). Finer-scale studies such as that of Chow et al. (2015) could be used to investigate this hypothesis, if data about the horizontal displacement are available (not reported by Chow et al. 2015). In our study, the 4 eels tracked into the Sargasso Sea in 2015 seemed to be tracking isotherms during the day (different ones before and after crossing the Gulf Stream). This was also reported for European eels in the Atlantic, although the isotherms tracked were not the same (Righton et al. 2016). However, it was not observed for the 2 eels tracked for the longest durations in 2014 nor for 2 other eels tracked for several days in the open ocean in 2015 and for which the thermohaline structure of the water column was similar to that experienced by the 4 eels tracked to the Sargasso Sea.

An important variability in the upper nighttime migration depth reached by eels is also highlighted in this study. Among the eels tracked in the open ocean, some ascended into waters much shallower than 100 m at night (up to the surface) while others never reached waters shallower than 100 m (200 m in the Sargasso Sea). The 2 eels tracked in the open ocean in 2014 ascended into very shallow waters at night, swimming above or around the mixed layer depth, as did 2 eels tracked for a short time in 2015, while the 4 eels tracked for the longest durations in 2015 remained in deeper water, swimming much deeper than the mixed layer depth. The variability observed here cannot be explained by the thermohaline structure of the water column (as for the daytime migration depth). Eels swimming in shallower waters experienced higher temperature. As already suggested in previous tracking studies (e.g. Amilhat et al. 2016), it seems that the occupation of certain thermal habitats may be a consequence, rather than a driver, of DVM. Most telemetry studies observed that eels migrating in the open ocean usually avoid the upper 100–150 m of the water column during the

night (Jellyman & Tsukamoto 2002, 2005, 2010, Aarestrup et al. 2009, Manabe et al. 2011, Schabetsberger et al. 2013). However, evidence of individuals ascending into much shallower water has been reported for *A. dieffenbachii* (Jellyman & Tsukamoto 2010), *A. japonica* (Manabe et al. 2011) and in the present study. It was mentioned that such individuals ascending into shallow waters ‘may have been affected by longer holding periods before release and more invasive attachment or implantation techniques’ (Schabetsberger et al. 2016, p. 151). Such an explanation clearly does not apply in the present study, as both behaviours were observed for individuals handled and equipped with PSATs using the same method. It has been suggested that the nighttime ascents into shallow water could be related to navigation to the Sargasso Sea, but no potential mechanism has been proposed (Aarestrup et al. 2009, Amilhat et al. 2016, Schabetsberger et al. 2016). Nevertheless, our study shows that eels are able to navigate toward the spawning area regardless of the depth of their nighttime ascents. As previously mentioned, our study also showed that eels had a higher activity at night than during the daytime period (present but not recognized in other eel telemetry studies). The significance of such behaviour is unknown. The study of Watanabe et al. (2016), who radio-tracked mature *A. celebesensis* and *A. marmorata* in an Indonesian lake during the pre-migration period and in absence of food and predators, suggested that the repeated up and down movements would be the result of the eels’ internal motivation for continuous swimming and is possibly energetically more efficient than if they keep swimming at a certain depth. Chow et al. (2015), who acoustically tracked maturing *A. japonica* close to their spawning area, suggested that migrating eels must keep swimming in order to avoid sinking, and their depth control must primarily depend on hydrodynamic lift controlled by the angle of their pectoral fins. However, they also suggested that the uppermost swimming depth (150–250 m) shared by different eel species could be partially determined by the pressure–swimbladder size relation, as the swelling swimbladder may act to gain buoyancy.

In our study, no relationship between the shallower nighttime migration depth and the lunar cycle was revealed. However, in several studies, a significant relationship was observed, with eels going deeper during the full moon than during the new moon (observed for *A. japonica*: Chow et al. 2015; *A. megastoma* and *A. marmorata*: Schabetsberger et al. 2013, 2015). A moon effect could have been masked in our

study because of the high cloud cover recorded during the tracking period or might not be discernible because temperate waters are not as clear as tropical waters (Schabetsberger et al. 2015).

The overall tracking success achieved in our study was higher in 2015 relative to 2014. Indeed, the cumulative number of days of tracking reached 402 in 2015 (N = 15 eels) vs. 222 d (N = 14, excluding 1 tag that never reported), and the cumulative reconstructed tracking distance reached circa 19 700 km in 2015 vs 8780 km in 2014. Although the longest and closest track to the spawning area was obtained in 2014 (Béguer-Pon et al. 2015), 4 eels were tracked in the Sargasso Sea in 2015 vs. only 1 in 2014. Among the factors that could contribute to such a difference in the tracking success, the release location could have played a decisive role. Eels tracked in 2015 were released directly over the Laurentian Channel, at Cabot Strait, i.e. over depths greater than in 2014 (200 vs. 80 m), where the outflow of the Laurentian Channel current naturally favours a faster departure from coastal waters, and at a location eels would have had to migrate through if they had not been translocated. Among eels released at Cabot Strait, those that used the Laurentian Channel reached the shelf edge faster than those that did not use it. Although the 2 different paths over the shelf did not seem to affect the southeastward orientation observed once off the shelf, spending less time over the continental shelf could be a good strategy for minimizing the risk of predation previously observed in continental/coastal waters (Béguer-Pon et al. 2012). Why half the eels released at the Cabot Strait used the deep Laurentian Channel and performed DVM while the other half remained on the continental shelf and performed erratic dives is unknown. Did the eels use the Laurentian Channel because they immediately performed DVM or did they perform DVM because they 'randomly' swam along/over the deep channel? In any case, DVM does not seem to be obligatory to reach open waters off the shelf.

Our study reports strong evidence of predation in coastal waters by homeothermic fish (2 cases) and 9 cases of suspected predation by pelagic predators (32 % of tracked eels). Clear predation and suspected predation events were also highlighted in tracking studies of European eels at sea (sharks, ectothermic fish and marine mammals: Aarestrup et al. 2009, Wahlberg et al. 2014, Westerberg et al. 2014, Wysujack et al. 2015, Amilhat et al. 2016, Righton et al. 2016) and Japanese eels (shark and tuna: Manabe et al. 2011). The possibility that PSATs themselves may increase the eels' susceptibility to predation cannot

be discounted and has already been discussed by e.g. Béguer-Pon et al. (2012, 2015). It nevertheless raises the possibility that predation during the spawning migration represents a significant source of mortality, and further studies are required to better understand this essential parameter of population dynamics.

CONCLUSIONS

With 7 additional eels tracked in the open ocean in 2015, including 4 tracked into the Sargasso Sea, we obtained new insights into the spawning oceanic migration of the American eel. Comparison with data obtained from similar tracking experiments conducted in 2014 illustrated the importance of observing a greater number of eels and the necessity of repeating the experiments over several years. In general, trajectories toward the eastern part of the presumed spawning area were similar, but vertical migration patterns, particularly the nighttime migration depth, differed significantly between years. The causes of such differences remain to be clarified, since the environmental parameters considered in this study did not shed light on this. Vertical migration behaviour did not seem to influence the migratory route followed by American eels, so it appears not to play a major role in the orientation mechanism. The behavioural variability observed in our study suggests considerable behavioural plasticity in the face of variability in oceanic environmental parameters. Additional observations are required to better document these newly revealed migratory patterns. Going from the raw data gathered by the PSATs to the trajectories followed by the eels, and then to the patterns of environmental variables experienced by them, requires an extensive use of models that, at each step, add a little more uncertainty to the next outcome. Finer-scale studies that would allow linking horizontal displacement with vertical swimming behaviour are also required to understand the reasons for the various vertical behaviours observed in this study.

Acknowledgements. This paper is a contribution of the Ocean Tracking Network (OTN). OTN is supported through a strategic network grant (NETGP no. 375118-08) from the Natural Sciences and Engineering Research Council (NSERC) of Canada with additional support from the Canada Foundation for Innovation (CFI, Project no. 13011). We thank Georges-Henri Lizotte, the fisherman who provided us with precious eels, as well as boat captains Lee MacKinnon and Darrin Baker. We also acknowledge Serge Higgins and Kyoko Ohashi, who participated in the field experiments.

LITERATURE CITED

- ✦ Aarestrup K, Økland F, Hansen MM, Righton D and others (2009) Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science* 325:1660
- ✦ Amilhat E, Aarestrup K, Faliex E, Simon G, Westerberg H, Righton D (2016) First evidence of European eels exiting the Mediterranean Sea during their spawning migration. *Sci Rep* 6:21817
- ✦ Aoyama J (2009) Life history and evolution of migration in catadromous eels (genus *Anguilla*). *Aqua-Biosci Monogr* 2:1–42
- Béguer-Pon M, Castonguay M, Benchetrit J, Hatin D and others (2014) Large-scale migration patterns of silver American eels from the St. Lawrence River to the Gulf using acoustic telemetry. *Can J Fish Aquat Sci* 71:1579–1592
- ✦ Béguer-Pon M, Benchetrit J, Castonguay M, Aarestrup K, Campana SE, Stokesbury MJW, Dodson JJ (2012) Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence. *PLOS ONE* 7: e46830
- ✦ Béguer-Pon M, Castonguay M, Shan S, Benchetrit J, Dodson JJ (2015) Direct observations of American eels migrating across the continental shelf to the Sargasso Sea. *Nat Commun* 6:8705
- ✦ Béguer-Pon M, Shan S, Thompson K, Castonguay M, Sheng J, Dodson JJ (2016) Exploring the role of the physical marine environment in silver eel migrations using a biophysical particle tracking model. *ICES J Mar Sci* 73:57–74
- ✦ Bianchi D, Galbraith ED, Carozza DA, Mislan KAS, Stock CA (2013) Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat Geosci* 6:545–548
- ✦ Brierley AS (2014) Diel vertical migration. *Curr Biol* 24: R1074–R1076
- ✦ Burgerhout E, Tudorache C, Brittijn SA, Palstra AP, Dirks RP, van den Thillart GEEJM (2013) Schooling reduces energy consumption in swimming male European eels, *Anguilla anguilla* L. *J Exp Mar Biol Ecol* 448:66–71
- ✦ Castonguay M, Hodson PV, Couillard CM, Eckersley MJ, Dutil JD, Verreault G (1994) Why is recruitment of the American eel, *Anguilla rostrata*, declining in the St. Lawrence River and Gulf? *Can J Fish Aquat Sci* 51: 479–488
- ✦ Chow S, Okazaki M, Watanabe T, Segawa K and others (2015) Light-sensitive vertical migration of the Japanese eel *Anguilla japonica* revealed by real-time tracking and its utilization for geolocation. *PLOS ONE* 10:e0121801
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2012) COSEWIC assessment and status report on the American eel *Anguilla rostrata* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON
- ✦ de Boyer Montégut C, Madec G, Fischer AS, Lazar A, Iudicone DCC (2004) Mixed layer depth over the global ocean: an examination of profile data and a profile-based climatology. *J Geophys Res* 109:C12003
- ✦ Fuglister FC, Voorhis AD (1965) A new method of tracking the Gulf Stream. *Limnol Oceanogr* 10:R115–R124
- ✦ Huisman J, Verhelst P, Deneudt K, Goethals P and others (2016) Heading south or north: novel insights on European silver eel *Anguilla anguilla* migration in the North Sea. *Mar Ecol Prog Ser* 554:257–262
- IUCN (2014) *Anguilla rostrata*. In: The IUCN Red List of Threatened Species Version 2014.3. www.iucnredlist.org (accessed on 21 November 2014)
- ✦ Jellyman D, Tsukamoto K (2002) First use of archival transmitters to track migrating freshwater eels *Anguilla dieffenbachii* at sea. *Mar Ecol Prog Ser* 233:207–215
- ✦ Jellyman D, Tsukamoto K (2005) Swimming depths of offshore migrating longfin eels *Anguilla dieffenbachii*. *Mar Ecol Prog Ser* 286:261–267
- ✦ Jellyman D, Tsukamoto K (2010) Vertical migrations may control maturation in migrating female *Anguilla dieffenbachii*. *Mar Ecol Prog Ser* 404:241–247
- ✦ Jessop BM (2010) Geographic effects on American eel (*Anguilla rostrata*) life history characteristics and strategies. *Can J Fish Aquat Sci* 67:326–346
- Kelley D (2014) oce: Analysis of oceanographic data. R package version 0.9-14. <http://CRAN.R-project.org/package=oce>
- Kleckner RC, McCleave JD (1985) Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current systems. *Dana* 4:67–92
- ✦ Kleckner RC, McCleave JD (1988) The northern limit of spawning by Atlantic eels (*Anguilla* spp.) in the Sargasso Sea in relation to thermal fronts and surface water masses. *J Mar Res* 46:647–667
- ✦ Kuroki M, Marohn L, Wysujack K, Miller MJ, Tsukamoto K, Hanel R (2017) Hatching time and larval growth of Atlantic eels in the Sargasso Sea. *Mar Biol* 164:118
- ✦ Manabe R, Aoyama J, Watanabe K, Kawai M, Miller MJ, Tsukamoto K (2011) First observations of the oceanic migration of Japanese eel, from pop-up archival transmitting tags. *Mar Ecol Prog Ser* 437:229–240
- ✦ Miller MJ, Tsukamoto K (2017) The ecology of oceanic dispersal and survival of anguillid leptocephali. *Can J Fish Aquat Sci* 74:958–971
- ✦ Miller MJ, Bonhommeau S, Munk P, Castonguay M, Hanel R, McCleave JD (2015) A century of research on the larval distributions of the Atlantic eels: a re-examination of the data. *Biol Rev Camb Philos Soc* 90: 1035–1064
- Mugge VMR (2015) Regression models with breakpoints/change-points estimation. Package 'segmented'. <https://cran.r-project.org/web/packages/segmented/segmented.pdf>
- ✦ Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv Mar Biol* 26:115–168
- Okamura A, Yamada Y, Yokouchi K, Horie N and others (2007) A silvering index for the Japanese eel *Anguilla japonica*. *Environ Biol Fishes* 80:77–89
- Paul J, Perruche C, Hameau A, El Moussaoui A (2016) Product user manual for Global Biogeochemical Analysis and Forecasting Product. GLOBAL_ANALYSIS_FORECAST_BIO_001_014., CMEMS version scope: Version 3.0. EU Copernicus Marine Service. <http://marine.copernicus.eu/>
- ✦ Putman NF, Scanlan MM, Billman EJ, O'Neil JP and others (2014) An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr Biol* 24:446–450
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Righton D, Westerberg H, Feunteun E, Økland F and others (2016) Empirical observations of the spawning migration of European eels: the long and dangerous road to the Sargasso Sea. *Sci Adv* 2:e1501694
- ✦ Rypina I, Llopiz JK, Pratt LJ, Lozier MS (2014) Dispersal pathways of American eel larvae from the Sargasso Sea. *Limnol Oceanogr* 59:1704–1714

- Rypina II, Pratt LJ, Lozier MS (2016) Influence of ocean circulation changes on the inter-annual variability of American eel larval dispersal. *Limnol Oceanogr* 61:1574–1588
- Schabetsberger R, Økland F, Aarestrup K, Kalfatak D and others (2013) Oceanic migration behaviour of tropical Pacific eels from Vanuatu. *Mar Ecol Prog Ser* 475:177–190
- Schabetsberger R, Økland F, Kalfatak D, Sichrowsky U and others (2015) Genetic and migratory evidence for sympatric spawning of tropical Pacific eels from Vanuatu. *Mar Ecol Prog Ser* 521:171–187
- Schabetsberger R, Miller MJ, Dall'Olmo G, Kaiser R and others (2016) Hydrographic features of anguillid spawning areas: potential signposts for migrating eels. *Mar Ecol Prog Ser* 554:141–155
- Sébert ME, Amerand A, Vettier A, Weltzien FA, Pasqualini C, Sébert P, Dufour S (2007) Effects of high hydrostatic pressure on the pituitary-gonad axis in the European eel, *Anguilla anguilla* (L.). *Gen Comp Endocrinol* 153:289–298
- Tesch FW (2003) *The eel*. Blackwell Publishing, Oxford
- Wahlberg M, Westerberg H, Aarestrup K, Feunteun E, Gargan P, Righton D (2014) Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration. *Deep-Sea Res I* 86:32–38
- Watanabe YY, Arai T, Limbong D, Mberato Y, Miyazaki N (2016) Repeated vertical movements of mature anguillid eels in a lake. *Mar Freshw Res* 67:1569–1574
- Westerberg H (1984) Diving behaviour of migrating eels studied by ultrasonic telemetry. In: Kimmich HP, Klewe HJ (eds) *Biotelemetry*, Vol VIII. Döring, Braunschweig, p 367–370
- Westerberg H, Sjöberg NB, Lagenfelt I, Aarestrup K, Righton D (2014) Behaviour of stocked and naturally recruited European eels during migration. *Mar Ecol Prog Ser* 496:145–157
- Wysujack K, Westerberg H, Aarestrup K, Trautner J, Kurwie T, Nagel F, Hanel R (2015) The migration behaviour of European silver eels (*Anguilla anguilla*) released in open ocean conditions. *Mar Freshw Res* 66:145–157
- Yamashita Y, Kitagawa D, Aoyama T (1985) Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel *Ammodytes personatus*. *Bull Japan Soc Sci Fish* 51:1–5

Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: March 22, 2017; Accepted: October 21, 2017
Proofs received from author(s): December 17, 2017