

NOTE

Oceanic Water Temperatures Less Than 20°C May Partly Account for Bias in American Eel Elver Otolith Age Estimates

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Abstract

The mystery of the discrepancy between American Eel *Anguilla rostrata* larval, glass, and elver ages derived from otolith examination and from observed spawning and recruitment dates is long standing. A variety of solutions have been proposed but none have been validated. Japanese Eels *Anguilla japonica* do not deposit daily otolith growth rings at water temperatures $\leq 10^\circ\text{C}$ and have less than daily deposition at temperatures 10–20°C, which may apply to American Eels. Oceanic water temperatures $\leq 10^\circ\text{C}$ between continental sites and the Gulf Stream during glass and elver eel migration periods have little effect on ages imputed from otolith ring counts of eels migrating to sites south of Cape Hatteras because coastal water temperatures infrequently, and usually only for a few days, decline below 10°C between Cape Hatteras and South Carolina. Coastal and estuarine water temperatures of 10–20°C may have more effect. North of Cape Hatteras, the temperature effect on otolith ages increased with distances north of and from the Gulf Stream. Adjustment to otolith ages for low estuarine/freshwater temperatures may more fully account for the difference between otolith and observed ages over the recruitment period at sites north and south of Cape Hatteras. The effect of recent higher oceanic water temperatures north of Cape Hatteras on otolith daily growth increments remains to be learned but may increase otolith age estimates. Otolith ages for glass and elver American Eels should be used with caution unless adjusted for seasonal low oceanic, estuarine, and freshwater temperatures; even then otolith aging issues remain. A greater understanding of oceanic migratory paths and durations is needed for American Eels.

islands (Benchetrit and McCleave 2015). Eels are catadromous, semelparous species, with juvenile, yellow-stage eels inhabiting estuaries and inland freshwaters during their continental growth phase until beginning sexual maturation as silver eels, migrating to oceanic waters, and spawning in the Sargasso Sea. American Eels spawn between fronts that are characterized by steep thermal and salinity gradients within the subtropical convergence zone (Kleckner and McCleave 1988; Munk et al. 2010; Chang et al. 2020), with American Eels spawning more westward and European Eels *Anguilla anguilla* more eastward (Westerberg et al. 2018). Although natural eel spawning has not been observed in the Sargasso Sea, its timing has been inferred by indirect methods such as larval size distributions and backward extrapolation of growth rates. Spawning by American Eels may begin as early as mid-January and peak between February and April, with an estimated peak of March 17 (Miller et al. 2015) or between December and March with a peak of February 6 (Westerberg et al. 2018), a difference of 39 d. Given an incubation period for American Eel ova of 32–45 h at 20°C (Oliveira and Hable 2010) and Sargasso Sea water temperatures during the spawning period averaging 23–25°C (Jessop 2020), the time of spawning is essentially the time of hatch relative to the oceanic migration period. Eel larvae (leptocephali) may enter the Florida Current directly from the Sargasso Sea between southern Florida and Cape Hatteras (Kleckner and McCleave 1982) and, perhaps, even into the Gulf Stream north of Cape Hatteras. The seasonally variable (peak flows during August–September) Antilles

The American Eel *Anguilla rostrata* is widely distributed in Atlantic continental North America, Mexico, and northern South America as well as the Caribbean

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Current may contribute larvae primarily between 28.5–30.5°N (mid to northern Florida), and a few may enter via the Gulf of Mexico (Kleckner and McCleave 1982, 1985; McCleave 1993; Miller et al. 2015; Domingues et al. 2019; Meinen et al. 2019). Crossing and detraining from the Florida Current, which becomes the Gulf Stream north of Cape Hatteras, may occur by active swimming for American Eels (Rypina et al. 2014; Miller et al. 2015), assisted by entrainment in warm core rings north of Cape Hatteras (Kleckner and McCleave 1985; Jessop 2020) and more broadly by submesoscale frontal exchange via bilateral mixing (Wenegrat et al. 2020). Larvae metamorphose to glass (unpigmented) eels over a period of 18–41 d (mean = 31 d; Arai et al. 2000) as they encounter the continental shelf (Kleckner and McCleave 1985). Glass eels, which become pigmented elvers soon after entering estuaries and continental streams, recruit increasingly later in the year, and at greater lengths, as latitude increases (Wang and Tzeng 1998; Jessop 2010).

The Atlantic coast of North America, continental shelf, and the Gulf Stream all curve northeastward at different rates with separation distances generally increasing northward. The departure locations of larval and glass eels from the Florida Current and Gulf Stream to any continental site are unknown and probably vary widely both north and south of the shortest distance between continental site and Gulf Stream. What triggers the departure of larvae from the Gulf Stream at any point is unknown, but Jessop and Lee (2016) and Jessop (2020) have proposed a genetically-based tendency to depart the Gulf Stream at latitudes corresponding to parental continental residence, which is consistent with genetic differences between glass eels of different geographic origins (Coté et al. 2014) and the imprinting of a magnetic map during larval migration to coastal streams (Naisbett-Jones et al. 2017). The maximum northerly extent of the Gulf Stream is about 42°N between 50–56°W, south and west of the Grand Banks off Newfoundland, beyond which it divides—with a complex pattern of eddies, meanders, and recirculations—into the northeastward-flowing North Atlantic Current and a southeastward-flowing branch that links with the Azores Current (Reverdin et al. 2003; Chang et al. 2020).

The mean durations of American Eel larval and glass eel oceanic phases (recruitment period) increase northward along the Atlantic coast but are of uncertain length. Bonhommeau et al. (2010) estimated the recruitment period as about 9.7 months by cohort and growth curve analyses of larval sampling in the Sargasso Sea (e.g., Boetius and Harding 1985; Kleckner and McCleave 1985), as about 6.2 months from daily otolith ring counts (e.g., Wang and Tzeng 1998, 2000; Arai et al. 2000; Powles and Warlen 2002), and as about 9 months to less than 1 year from numerical modeling (e.g., Haro and Krueger 1988; Kettle and Haines 2006). Estimates of the recruitment period

defined as the time between the mean spawning period and first recruitment to continental shores range from about 11 months to Florida to about 15 months to Nova Scotia (Jessop 2020).

A key assumption of the otolith aging method is that otolith rings represent daily depositions, which may not occur in the metamorphosis zone of leptocephali (Wang and Tzeng 2000; McCleave 2008) or at water temperatures that are low enough to influence the daily growth rate (Fukuda et al. 2009). Otolith growth and ring deposition in Japanese Eel *Anguilla japonica* glass eels and elvers ceased at water temperatures $\leq 10^{\circ}\text{C}$, was less than daily (0.455 rings/d) at 15°C , and was daily (1.01 rings/d) at $20\text{--}30^{\circ}\text{C}$ (Fukuda et al. 2009), which may apply to American Eels although a confirmatory study has not been done. Daily increments are deposited in American glass eels at water temperatures above 18°C (Martin 1995; Cieri and McCleave 2001). Daily growth increments have been assumed for Atlantic eel leptocephali at water temperatures $\geq 20^{\circ}\text{C}$ but have not been verified (Bonhommeau et al. 2010). Whether daily ring deposition occurs during the leptocephalus–glass eel metamorphosis period is uncertain (Wang and Tzeng 2000; McCleave 2008).

This study examines the relationship between the proportion of oceanic water temperatures $\leq 10^{\circ}\text{C}$, $10\text{--}15^{\circ}\text{C}$, and $15\text{--}20^{\circ}\text{C}$ from the Gulf Stream to continental streams as an adjustment factor for otolith daily ring counts (putative age in days) for American Eel elvers from the data in Table 3 of Wang and Tzeng (1998, 2000). It also examines the potential effect for American Eels of different departure points from the Gulf Stream to a continental site and of estuarine and lower stream water temperatures prior to capture.

METHODS

Study sites.—Wang and Tzeng (1998, 2000) provide estimates of recruitment period based on otolith daily ring counts for sites along the Atlantic coast of North America (Figure 1). Exact locations for sites R2 and R3 were not given, so the Guana River Dam, Florida (FL), was taken to represent R2 and Black Creek, Beaufort Inlet, North Carolina (NC), to represent R3. Both sites are, or have been, fished for elvers in the Atlantic States Marine Fisheries Commission (ASMFC) Eel Young-of-the-Year (YOY) program (L. M. Lee, North Carolina Division of Marine Fisheries, personal communication). The Guana River Dam is about 16 km upstream of the St. Augustine Inlet to the Tolomato River. The millpond at Black Creek where the fishery occurs is about 27 km upstream from the entrance to Beaufort Inlet, NC, and 9.5 km upstream of the mouth of the Newport River. The Annaquatucket River, Rhode Island (RI) collection site is uncertain; the Musquash River, New Brunswick (NB), and the East

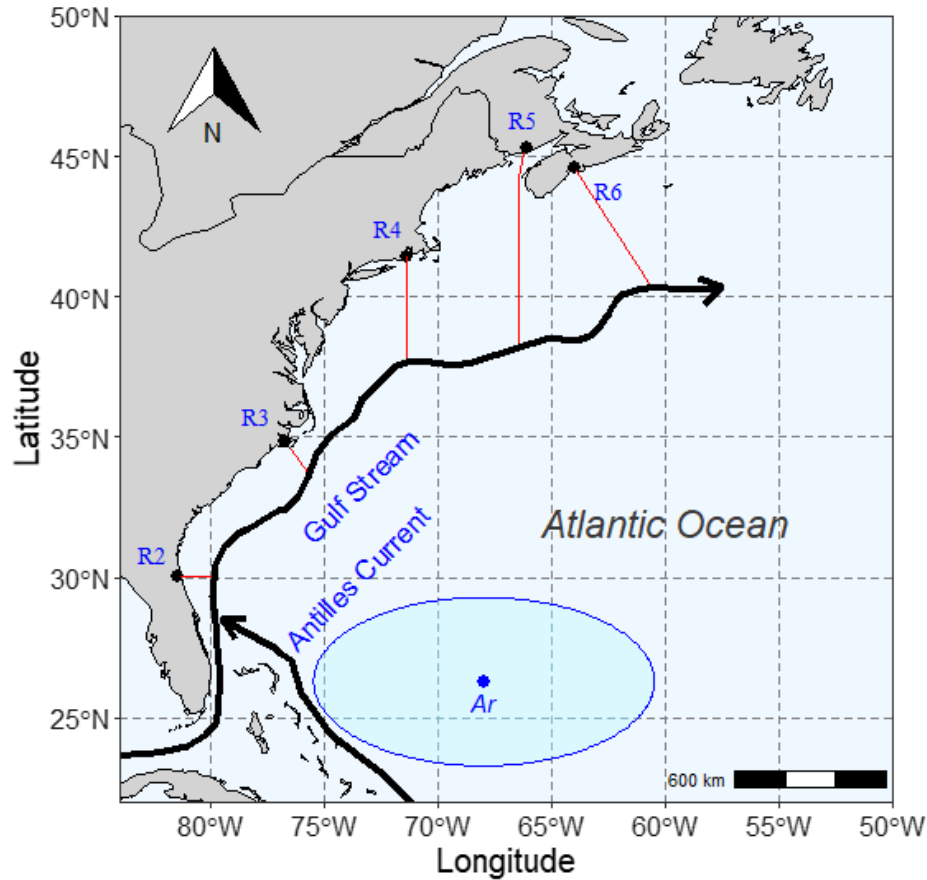


FIGURE 1. Sampling sites of American Eel elvers by Wang and Tzeng (1998, 2000), simplified migratory paths, and the center of spawning for American Eels (*Ar*).

River, Chester, Nova Scotia (NS), sites are near the head of tide.

For each site, the otolith age estimates (Tables 1 and 2) include mean total age (T_t) or recruitment duration, age at larval metamorphosis (T_m), and the difference between total age and age at metamorphosis from larva to glass eel (T_{t-m}), extracted from Table 3 of Wang and Tzeng (1998, 2000). The total observed migration time (T_{obs}) for each site was the difference between the spawning period mean estimate of February 6 (Westerberg et al. 2018) and the elver sampling date (Wang and Tzeng 1998, 2000). The start dates of annual elver runs from U.S. sites were obtained from the ASMFC Eel YOY database for the years 2000–2013, but not all years were sampled at each site and the sampling periods were quite variable. The start of the annual elver run to the Musquash River, NB, in 1996–1998 (R5) was obtained from commercial fishery records (M. Holland, Brunswick Aquaculture, personal communication) for the years 1996–1998 and from commercial fishery records (Atlantic Elver Fisheries Ltd., personal communication) for 1996–2019, excluding 2000 when no fishery occurred for the East River, Chester, NS

(R6). Little difference (–9 to +16 d) occurred between the sampling dates by Wang and Tzeng (1998, 2000) and those for the start of the elver run that were estimated from the ASMFC Eel YOY data, except for sites R3 and R6 where the differences were 48 and 30 d, respectively. This suggests late sampling dates relative to the run start, which is supported by the high mean pigmentation stage of the collected elvers. The run start date estimate for 1995 at all sites was based on the first 3 years of available data for each site, for example, 2000–2004 for sites R2–R4 and 1996–1998 for sites R5 and R6. The use of a mean spawning period of March 17 (Miller et al. 2015) rather than February 6 (Westerberg et al. 2018) was also examined.

The proportion of the American Eel migration period that was spent in the Sargasso Sea was estimated as the observed age (assuming a February 6 spawning peak) minus the otolith metamorphosis age (T_m) minus the travel time in the Gulf Stream minus the primary radial from each site to the Gulf Stream minus the sea surface temperature (SST)-adjusted T_{t-m} divided by the observed age. This assumes that the time to metamorphosis is accurate

TABLE 1. Site, spawning to coastal recruitment period (d) for otolith age estimates (T_t), time to metamorphosis (T_m), difference (T_{t-m}) between (T_t) and (T_m) from Wang and Tzeng (1998, 2000), observed recruitment ages (T_{obs}) assuming a mean spawning date of February 6, distance (km) from Gulf Stream to site, radial along which distance and water temperatures were measured, proportion of surface water temperatures $\leq 10^\circ\text{C}$ and $10\text{--}20^\circ\text{C}$ in 1995 between the western/northern edge of the Gulf Stream and continental site, sea surface temperature adjusted $T_t = T_{tadj}$, March 17 spawning date adjusted (T_{tsp}), and mean percentage difference between T_{obs} and T_t , T_{tadj} , and T_{tsp} . Ages have been rounded to whole days. FL = Florida, NC = North Carolina, RI = Rhode Island, NB = New Brunswick, and NS = Nova Scotia.

Site	T_t	T_m	T_{t-m}	T_{obs}	Distance	Radial ($^\circ$)	Proportion ($^\circ\text{C}$)			Percentage difference				
							≤ 10	10–15	15–20	T_{tadj}	T_{tsp}	$T_{obs}-T_t$	$T_{obs}-T_{tadj}$	$T_{obs}-T_{tsp}$
Guana River, FL (R2)	248	214	34	350	140	90	0	0	0.14	251	212	34.2	33.7	37.7
Black's Creek, NC (R3)	220	189	32	409	127	140	0	0	0.59	235	196	59.9	57.9	74.8
Annaquatucket River, RI (R4)	252	190	62	432	550	150	0.32	0.27	0.41	294	255	52.7	38.8	42.6
					475	180	0.37	0.32	0.32	294	255	52.7	37.6	42.8
					650	200	0.35	0.38	0.27	291	252	52.7	37.3	43.7
Musquash River, NB (R5)	272	193	80	446	750	150	0.57	0.23	0.20	345	306	48.3	28.4	31.5
					850	180	0.54	0.11	0.35	327	288	48.3	30.9	33.7
					950	210	0.66	0.11	0.24	341	302	48.3	27.9	29.7
East River, Chester, NS (R6)	284	211	72	428	850	125	0.46	0.16	0.38	343	304	40.6	22.3	24.9
					650	155	0.39	0.18	0.43	337	298	40.6	25.8	26.4
					695	185	0.52	0.24	0.24	375	336	40.6	12.8	14.6

TABLE 2. Correlations (r_{adj}) between seasonal mean SST ($^\circ\text{C}$) and year, sample size ($n=25$), statistical significance (P), difference in $^\circ\text{C}$ between 1995 and 2020 from a regression, and proportion $\leq 10^\circ\text{C}$ of the seasonal SST at 10 km distant from shore for five sites south (January 1 to March 31) and four sites north (January 1 to April 30) of Cape Hatteras (36°N) for the years 1995 to 2020.

Site	Latitude	Longitude	r_{adj}	P	Difference	Proportion $\leq 10^\circ\text{C}$
Guana River, FL (R2)	30.0286	81.2135	-0.64	<0.001	-3.3	0.0
Charleston, SC	32.6746	79.7963	-0.78	<0.001	-5.0	0.02
New River Inlet, NC	34.4594	77.2681	-0.74	<0.001	-6.4	0.11
Myrtle Beach, NC	33.6117	78.8052	-0.70	<0.001	-7.4	0.05
Black's Creek, NC (R3)	34.5901	76.6134	-0.72	<0.001	-4.9	0.02
Little Egg Inlet, NJ	39.4437	74.2024	0.15	0.48	0.4	0.75
Gilbert Stuart Brook, RI (R4)	41.3613	71.4129	0.30	0.14	1.1	0.95
Musquash River, NB (R5)	45.0529	66.2422	0.73	<0.001	2.4	1.0
East River, Chester, NS (R6)	44.3551	64.0970	0.53	<0.001	1.3	1.0

because most of it is in water temperatures $\geq 20^\circ\text{C}$ with the distance between the Gulf Stream and continental shelf adjusted for SST effects and that metamorphosis occurs near the continental shelf edge. All geographical distances (great circle) were measured with Google Earth Pro (2020).

Sea surface temperature.—Time series of daily SSTs ($^\circ\text{C}$; grid spacing of $0.25 \times 0.25^\circ$) were obtained for 1995 (the year of otolith sampling by Wang and Tzeng [1998, 2000]) from <https://mynasadata-las.larc.nasa.gov/EarthSystemLAS/UI.vm> for positions 20, 50, 100, 150, 200 km, and greater in 50-km increments as necessary along radials (degrees from north) between each elver collection

site and the Florida Current and Gulf Stream center (Table 1, Figure 1). Sea surface temperatures were unavailable prior to 1995 and were obtained during 1995 and 1996 for various time spans, based on elver run periods to each index site for 1–4 months prior to the elver sampling date at each site and increase in duration relative to the distance between the site and the Florida and Gulf Stream currents. Water temperatures along the radial from R2 were collected from January 1 to February 28, for R3 from January 1 to March 31, and from January 1 to April 30 for the radials from R4 to R6.

The primary distances from each site (river mouth at R2, entrance to Beaufort Inlet for R3, entrance to

TABLE 3. Migration periods and speeds for American Eels between the Sargasso Sea (SS) spawning area and continental sites based on estimated SS residence period and entrance to the Florida Current at about 28.5°N. The oceanic migration period is the time from departing the Gulf Stream to the continental site and the migration speed is based on straight line distances from the site to the Gulf Stream along primary radials (Figure 1).

Site	SS residence (d)	SS migration speed (km/d)	Oceanic migration period (d)	Oceanic migration speed (km/d)
Guana River, FL (R2)	214	5.82	136	1.04
Black's Creek, NC (R3)	176	7.07	228	0.56
Annaquatucket River, RI (R4)	165	7.55	257	2.17
Musquash River, NB (R5)	137	9.09	273	3.11
East River, Chester, NS (R6)	152	8.19	284	2.58

Narragansett Bay for R4, river mouth for R5, and entrance to Mahone Bay for R6) to the Gulf Stream were measured on specific radials: 90° for R2, 140° for R3, 180° for R4, 190° to the southern tip of Briar Island, NS, then 180° for R5, and 155° for R6. The effect of variability in departure point from the Gulf Stream to continental sites was examined by Gulf Stream distances and water temperatures along radials $\pm 30^\circ$ from each primary radial for sites north of Cape Hatteras, except -20° for R4 due to the Gulf Stream position north of Cape Hatteras. Distances from each site to the Gulf Stream were measured weekly from November 1 to March 1 of 2019–2020 for R2, January 5 to March 29 for R3, and January 5 to April 26 for R4 to R6. The distance from each site at which mean water temperatures became ≤ 10 , 10–15, and 15–20°C was used to determine the proportion of the mean distance between the site and the Gulf Stream used to adjust T_{t-m} to T_{adj} , the period of no or minimal otolith growth due to low water temperature, which was added to T_t to create T_{tadj} , the estimated total otolith age after adjustment for low water temperatures. The distances at each temperature interval were equivalent to the day intervals, assuming a constant migratory speed. The daily otolith increment adjustment factor for the interval $\leq 10^\circ\text{C}$ was 1.0 increment/d, for 10–15°C was $1 - 0.230 = 0.770$ increment/d (where 0.230 is the mean of 0.05 increment/d at 10°C and 0.455 increment/d at 15°C), and for the interval 15–20°C was $1 - 0.730 = 0.27$ increment/d (where 0.730 is the mean of 0.455 increment/d at 15°C and 1.005 increment/d at 20°C) on the basis that the mean number of increment/d at each temperature interval has been experienced and is included in total otolith age (T_t ; Fukuda et al. 2009). The difference from a daily increment is the adjustment factor. Daily increments at temperatures $\geq 20^\circ\text{C}$ were also assumed included in T_t . When a transition from one temperature interval to another occurred between two distance measurements, the mean distance was used. The mean percentage difference between T_{obs} and T_t indicates the mean difference between daily ages

estimated by otolith and by observed migration time (Table 1). North of Cape Hatteras, low SST effects on otolith age may apply to some leptocephali and metamorphosing leptocephali but primarily to glass eels and elvers because the northern limit of metamorphosing leptocephali is about 42°N and their eastward position was near or beyond the continental slope whereas glass eels mostly occurred over the continental shelf (Kleckner and McCleave 1985).

Sea surface temperatures were also obtained for 1995–2020 at 10 km offshore for January 1–April 30 from four sites north of Cape Hatteras (Little Egg Inlet, New Jersey [NJ]; the Annaquatucket River, RI [R4], in the Middle Atlantic Bight (MAB); the Musquash River, NB [R5], in the lower Bay of Fundy; and East River, Chester, NS [R6], along the Atlantic coast) and for January 1–March 31 at 10 km and 30 km offshore of five sites south of Cape Hatteras in the South Atlantic Bight (SAB; Beaufort Inlet, NC [R3]; New River Inlet, Onslow Bay, NC; Myrtle Beach, South Carolina [SC]; Charleston, SC; and Guana River, FL) to examine the presence of coastal SSTs $\leq 10^\circ\text{C}$ and any annual trend. Distances were measured approximately perpendicular to the coast at all sites.

River water temperatures between January 1, 2001 and March 31, 2005 were obtained for the Guana River Dam (R2) from the National Estuarine Research Reserve System Pine Island site (<http://cdmo.baruch.sc.edu/dges/>) located on the Tolomato River 4.9 km NE of the Guana River Dam. River water temperatures for January 1 to March 31, 2008–2012, were obtained from the U.S. Geological Survey (<https://waterwatch.usgs.gov/wqwatch>) sites at Waccamaw River near Longs, SC (USGS 02110500), about 210 km SW of Black River, NC, the presumed R3 site, and Lake Matamuskeet, NC, about 100 km NE of R3.

RESULTS

The difference between otolith ages (T_t) and observed ages (T_{obs}) was moderately explained (a reduction in mean

percentage difference of 16–25%) by adjustment for low marine water temperatures at sites north of Cape Hatteras, with minor (0.5–2%) explanation south of Cape Hatteras. Adjustment to the estimated elver age for the effect of SSTs between the Gulf Stream and continental sites increased with distance north of Cape Hatteras (sites R4–R6) and increased from south to north (Table 1). Minor (3.0% mean difference, range = 2.5–3.4%) variability occurred among the $T_{obs}-T_{adj}$ values along different radials from each of sites R4–R6. South of Cape Hatteras (sites R2–R3), SSTs $\leq 10^{\circ}\text{C}$ occurred infrequently and for a short period and distance and adjustment effects were minimal (Table 2). The distance along the Gulf Stream between the most distant site radials and their intersection (on January 5, 2020) with the Gulf Stream was 1,570 km. The choice of mean spawning date affected the percentage difference between the observed recruitment period and the recruitment period adjusted for SSTs and spawning date, with the March 17 date of Miller et al. (2015) increasing the percentage difference for $T_{obs}-T_{tsp}$ at all sites and decreasing from south to north (Table 1). The general decrease in $T_{obs}-T_{tadj}$ from south to north suggests that factors other than SST and spawning date affect otolith ages.

North of Cape Hatteras, the mean SSTs at 10 km offshore showed no significant increase between 1995 and 2020 at the sites (NJ, RI) in the MAB but significantly increased (range = 1.3–2.4°C) at the more northern lower Bay of Fundy and Atlantic coast sites (NB and NS; Table 2). South of Cape Hatteras in the SAB, SSTs 10 km offshore declined significantly (by -3.3°C to -7.4°C) at all sites but infrequently declined below 10°C at sites north of Florida and only in years after 2007. A similar pattern occurred for SSTs at 30 km offshore for sites south of Cape Hatteras, with annual declines in SST ranging from -3.6°C to -5.6°C and a reduced proportion of temperatures $\leq 10^{\circ}\text{C}$ at all sites (a proportion of 0.06 at New River Inlet and zero or near zero at all other sites). Recent mean SSTs vary -1°C to -3°C from 15°C at 10 km and 1°C to 2°C at 30 km, indicating that inshore waters are cooler than offshore waters.

Between January 1 and February 28 for the years 2001–2005, mean surface water temperatures ranged from 12.0°C to 17.3°C (minimums 7.5 – 14.2°C at the Pine Island hydrographic station proxy for the Guana River Dam [R2]). At the Waccamaw River, SC, the hydrographic station southern proxy for R3, mean January 1 to March 31 water temperatures for the years 2008–2012 ranged from 8.8°C to 13.1°C (minimums 1.6 – 6.9°C), while at the northern proxy Lake Matamuskeet, NC, site, mean water temperatures ranged from 6.4°C to 11.2°C (minimums -0.1 – 1.2°C).

The observed migration periods for American Eel elvers ranged from 1.17–1.22 years for sites north of Cape

Hatteras and 0.96–1.12 years for sites south of Cape Hatteras (Table 1). The estimated residence period within the Sargasso Sea for American Eels was estimated as 61.1% for site R2, 43.0% for R3, 38.2% for R4, 31.8% for R5, and 37.2% for R6. Sargasso Sea residence periods for more northerly sites ranged from 152 to 214 d (mean = 171 d) and tended to decrease, while migration speeds increased from the center of the spawning area to the junction of the Antilles Current with the Florida Current at about 28.5°N (about 1,340 km). Migration speeds to continental sites from the Florida Current and Gulf Stream increased southward and northward of site R3 (Table 3).

DISCUSSION

Substantial discrepancies occur between the otolith back-calculated ages of American eels and elvers and observed recruitment periods. McCleave (2008) and Bonhommeau et al. (2010) have reviewed the potential causes of the lower elver ages estimated from otolith analysis relative to the difference between estimated spawning dates and observed continental recruitment dates. These causes include (1) differences in larval cohort analysis due to use of length frequencies rather than ages; (2) uncertainties in the interpretation of otolith microstructure, with daily growth increments validated for glass and elver American Eels (Martin 1995; Cieri and McCleave 2001) but not for eel larvae, although otolith daily growth increments have been validated for Japanese larval and glass eels; (3) possible nondaily growth increments in eel larvae; (4) possible inadequate resolution of growth increments by light and scanning electron microscopy; and (5) difficulty in interpreting the diffuse metamorphic zone, where daily growth rings are not visible.

A moderate discrepancy occurs between the mean spawning times of American Eels estimated by different methods (Miller et al. 2015; Westerberg et al. 2018). At all sites, a mean spawning date of February 6 rather than March 17 best minimized the difference between otolith ages and observed ages. Spawning, of course, occurs over a wide range of dates and positions in the Sargasso Sea as does glass eel stream arrival, and these are not easily incorporated into a simple model examining SST effects on otolith-based elver ages.

Adjustment for SSTs ≤ 10 , 10–15, and 15 – 20°C on daily growth increments during passage from the Gulf Stream to continental shores for eel larvae detraining north of Cape Hatteras increased otolith ages by 22.0% (range = 15–32%), thereby reducing the difference between otolith-based and observed migration periods. Much of the discrepancy remaining might be due to estuarine and freshwater residence at temperatures $\leq 10^{\circ}\text{C}$ for uncertain periods prior to capture. For example, the large

differences between T_{obs} and T_{adj} (or T_i) for site R4 in the MAB might be partly explained by cold estuarine and stream water temperatures prior to the elver sampling. Wang and Tzeng (1998, 2000) do not state where in the Annaquatucket River (R4) the elver sample was taken, but the sample collection date (April 14) and elver pigmentation stages suggest that it might have been taken at the epitidal station. Delays of several weeks or longer may occur between the first arrival of glass eels into nearshore waters and subsequent movement upriver of glass eels and more-pigmented elvers in the colder waters and steeper gradient coastal topography north of Cape Hatteras (Haro and Krueger 1988; Jessop 2003). This may represent a period of physiological adjustment to estuarine conditions (Tesch 2003; Sorensen and Bianchini 1986; Haro and Krueger 1988) and a waiting period for environmental conditions (stream water temperatures of about $\geq 10^\circ\text{C}$ and appropriate discharge levels) that are suitable for river entry and upstream migration (Jessop 1998, 2003). Glass eels arrive in tidal waters in late January or early February and become abundant at the epitidal station about 4 weeks after becoming abundant at the tidal station (from March 14 to April 9; Haro and Krueger 1988). Water temperatures in the estuary remained $< 10^\circ\text{C}$ until the end of April and at the Hamilton Dam fishway until about mid-April, thereby adding perhaps between 28 and 56 d to the age of the elvers that was not recorded in the otolith daily rings. Glass eel and elver occurrence in such low estuarine and freshwater temperatures may be expected to increase the difference between true age and otolith daily ring deposition age. Accounting for a 56-d period reduces the percentage difference between T_{obs} and T_{adj} to 21.8% from 37.9%, a substantial change. Intertidal water temperatures at nine sites along the Atlantic coast of Nova Scotia remained $\leq 10.0^\circ\text{C}$ between January 1 and May 31 for the years 2015 to 2018 except for 1–3 d in mid to late May at one to four sites in 3 of 4 years (Scrosati and Ellrich 2020). The mean seasonal intertidal water temperatures across all years during this period generally increased from north to south along the Nova Scotia Atlantic coast from 1.94°C to 4.20°C (grand mean = 2.85°C). At site R6, elvers may be present in the upper estuary for at least several weeks prior to the start of the fishery, which begins about 16 d prior to upstream migration and capture at index traps, which are located about 100 m upstream of the fishery (travel times = 1.7–4.3 d; Jessop 2000, 2003, 2020).

South of Cape Hatteras, seasonal oceanic water temperatures have little explanatory effect (0.4–2.3% increase in temperature-adjusted otolith ages) and estuarine and river water temperatures may be more important, although the accuracy of otolith aging is questionable due to the large remaining difference between otolith age and observed age. Counting difficulties near the

metamorphosis area due to diffuse and obscure increments may result in undercounting of daily increments despite an adjustment procedure (Wang and Tzeng 2000). The large (57.9%) difference between T_{obs} and T_{adj} for site R3 and the smaller (33.7%) difference at site R2 may partly be due to lack of adjustment for estuarine and river water temperatures prior to elver sampling, but a substantial bias in otolith aging may also be responsible given the minimal distance between the Gulf Stream and sites, the substantial presence of SSTs $\geq 20^\circ\text{C}$ which are expected to support daily growth increments, and the absence of SSTs $< 15^\circ\text{C}$ which could have a large effect on otolith age adjustment. The observed water temperatures at the proxies for sites R2 and R3 were sufficiently low to explain a moderate portion of the difference between otolith and observed recruitment periods, depending upon the estuarine and freshwater residence periods prior to sampling. The duration of a staging period in estuarine waters and of freshwater migratory delays due to low water temperatures or high discharges for elvers south of Chesapeake Bay and Cape Hatteras is unknown. These would be influenced by the wider coastal plain, low gradient topography, and often longer estuaries than further north. Until such information is available, adjusting for the effects of low winter water temperatures on otolith daily increment production is not possible.

Larval, and presumably, glass eels occur at 50- to 300-m depths in oceanic waters (Castonguay and McCleave 1987). Continental shelf depths are typically 100–200 m north of Cape Cod, shallower over banks and deeper over basins, 50–100 m between Cape Cod and Cape Hatteras, and mostly < 50 m south of Cape Hatteras. Satellite-derived SSTs are highly correlated with water temperatures to at least 50 m (Chen and He 2015) and to greater depths (Chu and Fan 2000; Ali et al. 2004). Although winter water temperatures over the continental shelf increase slightly with depth, they typically remain $\leq 10^\circ\text{C}$ north of Cape Hatteras (Loder et al. 1998). The difference between SSTs and bottom water temperatures at the 25-m isobath for six sites in the MAB between Montauk Point, New York, and Chesapeake Bay, Virginia, varied around 0°C between January and March and was about 1– 2°C at all sites in April (Harding et al. 2008). In areas with strong tidal currents such as Georges Bank, Gulf of Maine, and Bay of Fundy, SSTs reflect the entire water column (Loder et al. 1998). The southwestward-flowing coastal Nova Scotia Current and shelf edge Labrador Current also transport cold water in winter at all depths along their paths.

Recruitment of American Eels from the Gulf Stream to sites along the Atlantic coast could occur from three general directions—northeastward, eastward, and southeastward. Each direction encounters variable conditions of distance, water temperature, and southward-flowing shelf

edge and coastal currents. The paths taken by eel larvae following departure from the Gulf Stream and glass eels following larval metamorphosis are unknown because there are no known techniques for tracking individuals or groups in the ocean. South of Cape Hatteras, glass eels could move westward directly from the Sargasso Sea or northwestward from the Florida Current/Antilles Current junction, or they could move south after a more northern exit via a coastal countercurrent running southward from Cape Hatteras (Soloviev et al. 2017) after being aided by periodic shoreward and shelf currents of about 0.12 m/s that occur every 2.5–5 d and persist for 0.5–4 d between mid fall and spring (Savidge 2002). Some might even pass through passages of the Greater Antilles into the Caribbean Sea, Gulf Loop Current, and eventually into the Florida Current (Miller et al. 2015). At R2, T_{obs} was lower (350 d) than at R3 (409 d), suggesting a shorter migration path to R2 if the times to exit the Sargasso Sea and cross the Florida current are comparable. The slow shoreward migration speeds south of Cape Hatteras are difficult to explain but may result from more northern departures while transiting the Gulf Stream due to its high velocity or an underestimated otolith T_m period and consequently underestimated Sargasso Sea residence period.

North of Cape Hatteras and south of the Cabot Strait, the coastal Nova Scotia Current and Scotian Shelf-edge extension of the Labrador Current, reinforced by Cabot Strait outflow, could both move glass eels southwestward while they approach and cross the continental shelf (Jessop 1998; Hannah et al. 2001; Chen and He 2015; Rutherford and Fennel 2018) unless they actively swim northwestward (or a combination of both occurs). The Nova Scotia Current and the shelf-edge current are strongest in winter, with limited cross-shelf transport of slope waters in the Scotian Shelf area (Rutherford and Fennel 2018). Winter–spring velocities of the southwestward-flowing Nova Scotia Current are about 0.06 m/s (5.2 km/d; Petrie 1987) and vary with depth, increasing from the surface at 0.04–0.06 m/s (3.5–5.2 km/d) to middepths (30–50 m) at 0.05–0.07 m/s (4.3–6.1 km/d) and decreasing near bottom (50–90 m) at 0.01–0.03 m/s (0.9–2.6 km/d; Smith 1987). Winter–spring velocities along the Scotian shelf edge extension of the Labrador Current average 6.1–6.8 km/d off southwestern Nova Scotia and are similar along the Scotian Shelf edge (Hannah et al. 2001). Complexity is added by gyres around some shelf banks. Departure from the Gulf Stream could also be more northerly and use southward-flowing shelf and coastal currents with velocities that decrease from north to south between the Scotian Shelf and Cape Hatteras. Current patterns and reduced swimming speeds due to low water temperatures (Veza et al. 2020) could help explain the relatively slow oceanic migration speeds at sites north of Cape Hatteras.

If eel larvae depart from the Gulf Stream north of Cape Hatteras and south of the continental stream, they ultimately enter as glass eels and active swimming and map navigation northwestward is required (Rypina et al. 2014; Cresci et al. 2017; Naisbet-Jones et al. 2017). Active swimming and map navigation may occur from other Gulf Stream departure points, including points south of Cape Hatteras. Movement across the continental shelf may be assisted by selective tidal stream transport (Jessop et al. 2001) in a process similar to that in estuaries (McCleave and Kleckner 1982). In the MAB, cross-shelf onshore flows at middepths and at near-bottom depths shoreward of the 50-m isobath (Lentz 2008) may also assist shoreward movement by glass eels. Whatever the Gulf Stream departure point, effect of continental shelf edge and coastal currents, and degree of active, directed swimming by glass eels, there is a clear pattern over several years in the timing of stream arrival and migratory period (earlier and longer from north to south) and commercial fishery catch abundance (increasing from north to south) around Atlantic coastal Nova Scotia and into the lower Bay of Fundy (NS, NB; Jessop 1998). Commercial catch data are presently unavailable due to privacy concerns to confirm that this pattern continues today. Continental arrival times are also annually consistent at more southern sites (ASMFC YOY program).

Since 1995 when the Wang and Tzeng (1998, 2000) elver samples were collected, the warming of coastal and oceanic waters west of the Gulf Stream has affected the timing of elver continental arrival north of Cape Hatteras, with recruitment becoming earlier at the East River, Chester, by 22 d between 1996 and 2018 (Jessop 2020), which could reduce T_{obs} in recent years. Between 1875 and 2007, Atlantic coastal mean annual water temperatures have increased about 1.0°C in the Gulf of Maine and about 0.7°C in the MAB (Shearman and Lentz 2010). The annual increase in mean seasonal SSTs at 10 km offshore in the lower Bay of Fundy, Atlantic coast of NS, and MAB are consistent with the above values.

Winter SSTs between 1875 and 2007 showed little change in the SAB south of Cape Hatteras (Sherman and Lentz 2010) although Caesar et al. (2018) found cooling or below-average warming in SST trends between 1870 and 2016. This study found winter SSTs at 10 km and 30 km offshore of SAB sites to have decreased significantly between 1995 and 2020, more so at inshore waters. Winter decreases in SSTs in coastal waters of the SAB north of about 31°N have been attributed to seasonal cooling due to northwest winds, freshwater runoff from coastal streams, and upward advection of cold shelf edge waters (Blanton and Chandler 1983; Mathews and Pashuk 1986). The irregularity and infrequency of SSTs $\leq 10.0^\circ\text{C}$ in the SAB imply minimal or no effect on eel otolith growth patterns, but SSTs between 10–20°C may have a greater effect.

The warming of coastal and oceanic waters inshore of the Gulf Stream has been linked to a northward and closer to shore shift of the Gulf Stream due to a weakening of the Atlantic meridional overturning (Caesar et al. 2018; Praetorius 2018). Oceanic warming since 1995 results in a decreasing ability to use water temperatures $\leq 10^{\circ}\text{C}$ and $10\text{--}20^{\circ}\text{C}$ to adjust for the postmetamorphic underaging by elver otoliths at recruitment at sites north of Cape Hatteras. Whether this warming will lead to increased post-metamorphic daily otolith increment counts (ages) remains to be learned.

Jessop (2020) estimated that 92–93% of the migratory period to sites south of Cape Hatteras was spent within the Sargasso Sea, while further northeastward times decreased progressively (81% to 69–70%). However, those estimates did not account for water temperature effects that may increase the pre- and postmetamorphic period and thus decrease the Sargasso Sea residence period. Accounting for SSTs gives much lower Sargasso Sea residence periods as a percentage of the observed migratory period—a high 61.1% for site R2 and 31.8% to 43.0% for all other sites. The dates for departing the Sargasso Sea for eel larvae from these sites (June 21 to September 6) are similar to sampling dates for larval eel in the Florida Current by Kleckner and McCleave (1982). Higher estimates for Sargasso Sea residence period would create lower estimates for oceanic migration period and vice versa. A definitive method to estimate Sargasso Sea residence period is needed.

Estimated migration speeds differ widely during different migration phases—within the Sargasso Sea, Gulf Stream entrainment, and between Gulf Stream and continental sites. Within the Sargasso Sea, high daily migration speeds could result from an underestimate of the time spent resident in the Sargasso Sea as well as from poorly measured irregular current patterns within the Sargasso Sea. Westerberg et al. (2018), based on passive larval drift, estimated a migration speed of about 4.3 km/d and a retention period for eel larvae of about 1 year, which is about double the retention time and slightly more than half the migration speed (7.5 km/d) estimated here for American Eels.

Within the southern Sargasso Sea, most of the currents tend westward and northerly into the Antilles Current that joins with the Florida Current (Munk et al. 2010; Domingues et al. 2019) and could contribute to the migration speed of larval eels. Most of the Antilles Current occurs west of about -76.5° longitude with a northward meridional velocity at -76.8° longitude of 30.2–34.6 km/d at about 400 m depth (Meinen et al. 2019). The current velocity was about 13.0–17.3 km/d at about 200 m and decreased rapidly towards the surface to 0.0–4.3 km/d at the surface where the current is highly variable and may periodically have a weak southward

flow. Leptocephali occurring at depths of 50–300 m (Castonguay and McCleave 1985) could use these currents. The eastward edge (about -76.4°) of the Antilles Current is about 900 km from the center of the American Eel spawning area (Meinen et al. 2019). The presence of large-scale Rossby wave-like features moving westward at about 7.8 km/d, such as the one detected at 26.5°N (Meinen et al. 2019), could transport larvae from the Sargasso Sea to the Antilles Current. More likely is that large anticyclonic eddies originating east of the Bahamas and Antilles Current that merge with the Florida Current between about $28\text{--}33^{\circ}\text{N}$ and influence its seasonal variability have a greater effect (Chelton et al. 2011; Domingues et al. 2019). Such nonlinear, mesoscale, anticyclonic eddies, primarily (about 75%) westward-propagating, can advect a parcel of trapped fluid that could transport eel larvae out of the Sargasso Sea and into the Florida Current and Gulf Stream anywhere between about $31\text{--}38^{\circ}\text{N}$ (Chelton et al. 2011; Penna and Gaube 2020). Little is known about the seasonal or annual frequency of mesoscale eddies within the Sargasso Sea area. An abundance of eddies may influence the speed of virtual larval (*v*-larvae) migration but the effect depends on *v*-larval swimming speed such that the movement speed of slower swimming *v*-larvae is increased and that of faster swimming *v*-larvae is slowed (Chang et al. 2017) while food attraction acts to retain faster swimming *v*-larvae and slower swimming *v*-larvae are passively retained (Chang et al. 2018). The effect of small eddies may also be important but has not been examined. Mesoscale eddy lifespan increases with amplitude (sea surface height), with the larger eddies having lifetimes ≥ 16 weeks (average 32 weeks) and propagating a mean of 550 km but may travel over 1,000 km at velocities of about 2.5 km/d. These observations may help explain the estimated migration speeds for larval eels within and departing the Sargasso Sea. The increase in migration speed for eels from continental sites further north may reflect variability in spawning timing and area for eels from different sites. Estimated mean oceanic migration speeds by American Eel larvae and glass eels between the Gulf Stream and continental sites both south and north of Cape Hatteras were much lower than the sustained swimming speed of 5.69 km/d for glass eels at water temperatures between 5°C and 15°C estimated by Wuenschel and Able (2008). Several reasons could account for this, including countercurrent effects, oceanic water temperatures lower than experimental water temperatures for part of the migration period, slower speeds by leptocephali than by glass eels, unaccounted for residence times in estuarine and lower river sites before capture at water temperatures that affect otolith aging, and unresolved otolith aging issues.

Clearly, elver otolith ages substantially underestimate the duration of the recruitment migration, which varies

geographically along the Atlantic coasts of North America, and they should be used with caution for the estimation of growth rate, migration period, and spawning times unless adjusted for seasonal oceanic, estuarine, and freshwater water temperatures. Further research is necessary to provide a means to adjust elver otolith ages for seasonal low estuarine/freshwater temperatures in the North Atlantic region to resolve lingering questions about otolith aging accuracy and to better understand oceanic migration routes.

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