Oceanic Environmental Effects on American Eel Recruitment to the East River, Chester, Nova Scotia

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Abstract
The effect of oceanic environmental conditions on the recruitment of American Eel Anguilla rostrata to coastal waters is poorly understood. This study examined correlations between the annual elver count index of the East River, Chester, Nova Scotia, seasonal oceanic environmental conditions associated with the larval and glass eel stages, and larval and glass eel migration times between the spawning area and continental recruitment. In recent years, the elver fishery of the East River has started earlier in conjunction with increasing inshore, continental shelf, and Gulf Stream water temperatures, with the strength of the correlation decreasing with distance from shore. A northward shift of the Gulf Stream may also have contributed to earlier arrival dates. Annual elver index values increased over the study period but were not significantly correlated with any atmospheric or oceanic environmental conditions, perhaps due to a relatively short time series, although effect sizes (correlation coefficient r) were often medium, a level potentially considered of biological importance. Elver mean lengths varied annually with no trend and were not significantly correlated with the elver index. Significant correlations occurred between the North Atlantic Oscillation and Sargasso Sea primary productivity (lag of 0) and Emerald Basin (Scotian Shelf) water temperatures (lag of –5), while Scotian Shelf chlorophyll values decreased with increasing water temperatures (lag of –3). The mean migration period from spawning to stream entrance at the East River was estimated at 1.2 years, mostly spent growing in and ultimately leaving the Sargasso Sea, then crossing oceanic and continental shelf waters between the Gulf Stream and coastal streams, with a short period of transport along the Gulf Stream. The estimate of total migration period based on observed recruitment times at various sites and the mean of the estimated spawning period averaged 45.5% greater than those estimated from otolith methods, perhaps due to the effect on otolith daily ring deposition during glass eel migration in oceanic water temperatures <10°C between the Gulf Stream and coast.

Relationships between continental recruitment of American Eel Anguilla rostrata and oceanic environmental factors, such as the Gulf Stream speed and position (Castonguay et al. 1994) and coastal water temperatures (Wang and Tzeng 1998), are poorly known. The recruitment of European Eel Anguilla anguilla has been more widely examined in relationship to the North Atlantic Oscillation (NAO) (Friedland et al. 2007) and primary production in the Sargasso Sea (Bonhommeau et al. 2008a). River passage obstructions, fishery exploitation,
pollution, and infection by the exotic swim-bladder parasite *Anguillicola crassus*, amongst other threats, have negatively influenced continental American Eel stock status (Chaput et al. 2014). Stock status varies regionally within Canada from increasing to no trend to a severe decline in abundance in the Saint Lawrence River basin, particularly in Lake Ontario partly due to historically inadequate upstream and downstream fish passage facilities at several hydroelectric dams in the upper St. Lawrence and Ottawa rivers (DFO 2014). Recent signs of recovery have occurred there and in parts of Atlantic Canada. The COSEWIC (2012) determination that the stock is “threatened” has not yet been accepted for listing under the Species at Risk Act by the Department of Fisheries and Oceans (DFO) and Environment and Climate Change Canada. Regulatory action has been taken to reduce the effects of commercial fishing within Canada and improve hydroelectric dam passage on the upper St. Lawrence River (DFO 2014). In the United States, the American Eel stock has been described as “not threatened or endangered” (USFWS 2007, 2015) but with a depleted abundance and stable trend in abundance (Shepard 2015).

The American Eel is catadromous and semelparous, with juvenile, yellow-stage eels inhabiting freshwaters and coastal estuaries and with the ages at sexual maturation increasing with latitude and being younger for males while older for females (Jessop et al. 2002; Jessop 2010; Cairns et al. 2014). Sexually maturing silver eels migrate to the Sargasso Sea to spawn and then die. Although American Eels are panmictic (Côté et al. 2013), genetically distinct ecotypes related to rearing habitat (brackish or saltwater and freshwater) occur (Pavey et al. 2015). American Eels may begin spawning as early as mid-January but do so mostly between February and April (Miller et al. 2015), although Westerberg et al. (2018) concluded that spawning occurs between December and March, peaking in early February. Spawning occurs at the western side of and between temperature fronts (northern temperature front at the 22.5°C isotherm) within the Subtropical Convergence Zone, the location of which may position larvae for access to west-flowing currents (Kleckner and McCleave 1988; McCleave 1993; Friedland et al. 2007; Munk et al. 2010; Westerberg et al. 2018). Larval eels (leptocephali) migrate from the Sargasso Sea to the Florida Current, perhaps via the poorly defined, winter-seasonal Antilles Current (Kleckner and McCleave 1985; McCleave 1993) but more generally at latitudes between northern Florida and South Carolina (about 30°N to 33°N). Abundance increases northward towards Cape Hatteras (Kleckner and McCleave 1982; McCleave 1993; Miller et al. 2015). The Florida Current becomes the Gulf Stream where it breaks from the continental shelf at Cape Hatteras. Within these currents, larval eels are carried along the Atlantic coast of North America before detraining as leptocephali and metamorphosing from leptocephali to “glass” (unpigmented) eels, presumably over the continental shelf (Tesch 1977; Otake et al. 2006) or in oceanic waters where the continental shelf is distant from the Gulf Stream, as off the mid-Atlantic states and Atlantic Canada (Kleckner and McCleave 1985). Leptocephali lengths in oceanic and continental shelf waters and eel sizes at continental stream entrances increase with increasing northern latitude (Wang and Tzeng 1998, 2000; Jessop 2010; Miller et al. 2015), implying that the timing of leptocephalus metamorphosis increases northward and determines size at continental recruitment. Exactly how leptocephali and glass eels reach and cross the continental shelf is uncertain, but larger leptocephali may actively swim during migration within the Sargasso Sea and crossing the Florida Current and Gulf Stream (Miller et al. 2015; Miller and Tsukamoto 2017). The assumption of active swimming with a preferred northwestern direction by leptocephali and glass eels throughout the migration period resulted in high success rates for reaching the continental shelf in a particle tracking modeling study (Rypina et al. 2014). European Eel (and presumably American Eel) leptocephali and glass eels may engage in active navigation by magnetic compass and map when crossing the Gulf Stream, during oceanic migration, and while crossing the continental shelf to enter coastal waters (Cresci et al. 2017; Naisbett-Jones et al. 2017). Further support for the active swimming hypothesis is provided by the fact that the predominant current flow direction of continental shelf and shelf–slope waters is southwest (Loder et al. 1998) via the Nova Scotia Current and extensions along the Scotian Shelf, into the Gulf of Maine, and southerly along the coast and the southern extension of the Labrador Current along the outer continental shelf. This would require glass eels to actively swim northwestern to reach streams north of Cape Hatteras or to detrain north and use shelf currents to move south. Glass eels are capable of more active swimming due to the morphological and physiological changes following metamorphosis (Miller and Tsukamoto 2017).

The factors initiating larval detrainment from the Florida Current and Gulf Stream are uncertain. Jessop and Lee (2016) hypothesized that the timing of larval detrainment and metamorphosis is governed by an internal biological clock that is related to maternal age and size, which in turn is correlated with latitude and distance from the spawning ground (Jessop 2010). Metamorphosis may be initiated over an extended period as larvae become developmentally competent or respond to an environmental cue (Kleckner and McCleave 1985), both of which may have geographic clines. The process of detrainment other than by active swimming also remains uncertain, but Kleckner and McCleave (1985) and Miller and Tsukamoto (2017) have hypothesized a role for warm-core eddies (rings) that detach to the northwest from the Gulf Stream north of Cape
This study examines whether the environmental (oceanographic and atmospheric) conditions experienced by American Eel larvae during their oceanic migration to continental waters may help explain patterns in glass eel recruitment as represented by annual elver index counts at the East River, Chester, Nova Scotia. Sea surface water temperatures, the NAO, Sargasso Sea primary productivity effects on early feeding larval survival, Atlantic coastal zone chlorophyll measurements (an indicator of primary productivity), and oceanic (within the Sargasso Sea and Gulf Stream) current velocities may all affect the survival and recruitment of American Eels (Castonguay et al. 1994; Friedland et al. 2007; Bonhommeau et al. 2008a, 2008b; Arribas et al. 2012; Miller et al. 2016). First examined are correlations between the annual elver index and seasonal oceanic environmental conditions related to the larval and glass eel stages and between potentially interrelated environmental conditions, which may reveal the determinants of elver mortality during migration and the success of continental recruitment. Next was examined larval and glass eel migration times between spawning and stream arrival and during various migration segments. The total migration period was calculated as the time between the mean spawning period (estimated as February 6 from Westerberg et al. [2018]) and the mean time of continental arrival based on the start of the run to the East River. Migration times to continental streams from the Gulf Stream were derived from the distances from the Gulf Stream to shore and glass eel swimming speeds from Wuenschel and Able (2008). Migration times within the Gulf Stream between intersecting radials from a geographic range of shore sites were estimated from a seasonal snapshot of mean current velocities between radials. Observed migration times were compared with values based on otolith daily rings (Wang and Tzeng 1998). Migration times within various segments of the total migration period are useful because they help to understand this phase of American Eel life history and may be applied to better quantify mortality during migration segments.

**METHODS**

**Study site.**—The East River, Chester, Nova Scotia, enters the Atlantic Ocean on the northeast side of Mahone Bay and has a watershed of 134.0 km² (Jessop 2003a). The annual elver index program at the East River was the first index of recruitment of American Eels to North American Atlantic coastal waters (Table 1; Figure 1), operating 1996–2001 and 2008–2018 (17 years to date), closed by the DFO between 2003 and 2007, and with 2002 omitted as unreliable index data (DFO 2010). The index consists of the total number of elvers in the counts from four traps, two on each side of the river, at the mouth of the
river just downstream of a small falls plus the commercial fishery catches downstream of the traps (Jessop 2003b; DFO 2010). Daily elver trap numbers were initially estimated volumetrically with calibrated aliquots (Jessop 2003a), but after 2015, catch volumes were replaced by catch wet weights for easier comparison with commercial catches (DFO 2017). The estimated elver index numbers are presented to the nearest elver for calculation purposes but the unquantified estimation errors are at least ±10,000 elvers (Jessop 2003b). Elver recruitment to the East River occurs primarily between mid-April and mid-July (Jessop 2003b), with a mean time of stream arrival of April 20 (range = March 18 to May 19). The commercial dip-net fishery typically starts before the trap counts begin (mean = 16 d; range = –10 to 34 d). Fishers are required by the DFO to maintain a logbook of daily catch (kg) wet weight and fishing effort (hours).

Limited fisheries occurred in 1999 and 2001, and no fishery occurred in 2000 due to poor market conditions. Biological data on length (to 0.1 mm), dry (blotted) weight, and pigment stage (Haro and Krueger 1988) were also collected for the years 1996–2001 (Jessop 2003b) and 2008–2018, excluding 2002 when there were data quality issues.

The start, mean, and end date of annual elver runs from U.S. sites (Figure 1) was obtained from the Eel Young-of-the-Year Database Excel file for the years 2000–2006, but not all years were sampled at each site and the sampling periods were quite variable (L. M. Lee, North Carolina Division of Marine Fisheries, personal communication). Exact locations were not given for sites R2 and R3 of Wang and Tzeng (1998) so data from the Guana River Dam was taken to represent Florida (site R2), Blacks Creek, Beaufort Inlet, North Carolina was taken to represent North Carolina (site R3), and Gilbert Stuart Brook, Rhode Island, substituted for unavailable data from the Annaquatucket River, Rhode Island (site R4). The start, mean, and end date of the annual elver run to the Musquash River, New Brunswick, during 1996–1998 (site R5) was obtained from commercial fishery records (M. Holland, Brunswick Aquaculture, personal communication); site R6 was the East River.

### Table 1

| Year | Elver index | Elver TL | NOA | Sargasso Sea temperature | Sargasso Sea PP | Gulf Stream temperature | Chlorophyll |
|------|-------------|----------|-----|--------------------------|----------------|-------------------------|-------------|
| 1995 | 1.0275      |          |     | 23.82                    | 3.759          | 21.00                   |             |
| 1996 | 1,124,065   | 62.02    | –0.8675 | 23.78                   | 4.629          | 20.20                   |             |
| 1997 | 1,477,611   | 64.93    | 0.0325 | 23.75                    | 3.185          | 20.89                   |             |
| 1998 | 436,052     | 60.13    | –0.2725 | 24.09                    | 2.797          | 20.64                   | 2.00        |
| 1999 | 448,781     | 58.90    | 0.2100 | 24.29                    | 3.536          | 21.49                   | 2.09        |
| 2000 | 791,204     | 60.14    | 0.8675 | 23.52                    | 3.641          | 21.25                   | 2.15        |
| 2001 | 593,248     | 61.67    | –0.6275 | 24.03                    | 3.256          | 20.69                   | 1.97        |
| 2002 | 0.0650      |          |     | 24.11                    | 4.699          | 21.26                   | 2.46        |
| 2003 | –0.2725     |          |     | 24.59                    | 5.313          | 21.05                   | 2.83        |
| 2004 | –0.0700     |          |     | 24.00                    | 3.907          | 20.91                   | 2.66        |
| 2005 | –0.1350     |          |     | 23.35                    | 4.386          | 20.55                   | 2.63        |
| 2006 | –0.5750     |          |     | 23.84                    | 4.292          | 20.45                   | 2.92        |
| 2007 | 0.2575      |          |     | 24.26                    | 3.606          | 21.80                   | 2.89        |
| 2008 | 1,896,079   | 60.25    | 0.2050 | 24.28                    | 3.046          | 21.91                   | 3.06        |
| 2009 | 1,058,814   | 58.93    | –0.2650 | 23.82                   | 3.822          | 21.27                   | 3.26        |
| 2010 | 559,218     | 58.85    | –1.9250 | 23.94                    | 5.741          | 21.01                   | 2.89        |
| 2011 | 2,100,789   |          |     | 23.50                    | 4.725          | 20.75                   | 3.49        |
| 2012 | 1,898,427   | 58.73    | 1.0175 | 24.05                    | 2.304          | 21.78                   | 3.43        |
| 2013 | 2,050,428   | 61.93    | –0.7725 | 24.13                    | 4.140          | 21.44                   | 3.32        |
| 2014 | 2,706,125   | 59.47    | 0.5325 | 25.22                    | 4.620          | 21.77                   | 3.09        |
| 2015 | 1,214,552   | 59.74    | 1.3425 | 25.04                    | 3.779          | 21.44                   | 3.29        |
| 2016 | 1,723,019   | 60.53    | 0.8350 | 25.16                    | 1.873          | 22.61                   | 3.35        |
| 2017 | 1,189,109   | 61.73    | 0.3630 | 24.63                    |               |                         | 3.52        |
| 2018 | 3,724,169   | 61.38    | 0.4650 | 24.84                    |               |                         |             |
Sea surface temperature.—A time series (1995–2018) of daily sea surface temperatures (SSTs; °C) were obtained from https://mynasadata-las.larc.nasa.gov/EarthSystemLAS/UI.vm for oceanic positions off the coast of Nova Scotia to assess the correlation between the start of the commercial elver fishery at the East River and coastal water temperatures (Figure 1). The sites were as follows: Mahone Bay (44.4°N, 64.1°W; period February 1 to April 30), Emerald Basin on the Scotian Shelf (43.99°N, 62.81°W; period February 1 to May 31), and the Gulf Stream at 37.9°N, 64°W due south of Mahone Bay (period December 1 to March 31). In 2018–2019, the mean measured Gulf Stream position between December 18 and January 31 was similar (37.87°N, 64.08°W) to that of the fixed water temperature measured position, and the Gulf Stream annual mean seasonal water temperatures are believed acceptable. Annual variability in the Gulf Stream north–south position is about 100 km, and the observed range in positions was 75 km (690–765 km). Other date ranges were examined for each site, and those with the highest correlation coefficient were used. These dates presumably indicate times of high glass eel presence. Annual mean SSTs were examined for each site.

Annual SSTs were obtained for various time spans, based on elver run periods to the nearest index site and leading by the approximate times to move from the Gulf Stream to the coast, for the Gulf Stream offshore of Goose Creek, South Carolina (site 2; 32.0°N, 79.0°W; December 1 to April 15), Cape Hatteras, North Carolina (site 3; 35.4°N, 74.1°W; January 1 to May 15), south of Cape Cod, Massachusetts (site 4; 37.4°N, 70.0°W; January 1 to May 15), south of Mahone Bay, Nova Scotia (site 5; 37.9°N, 64.1°W; February 1 to May 31), and Emerald Basin, continental shelf, Nova Scotia (site 6; 44.0°N; 62.8°W; January 1 to April 30) (Figure 1). The annual grand mean Gulf Stream SST at these sites was also estimated.
Sargasso Sea SSTs were obtained for a 3 x 3 rectangular grid of locations within the area bounded by 23°N to 28°N and 75°W to 58°W that defines the spawning area for American Eels for the spawning period December 15 to March 20 (Westerberg et al. 2018). The sites were as follows for row 1: 27.9°N, 74.1°W; 27.9°N, 69.1°W; and 27.9°N, 64.1°W; for row 2: 25.9°N, 74.1°W; 25.9°N, 69.1°W; and 25.9°N, 64.1°W; and for row 3: 23.9°N, 74.1°W; 23.9°N, 69.1°W; 23.9°N, 64.1°W. The grand mean annual SSTs for these sites were also estimated.

North Atlantic Oscillation.—A time series (1995-2018) of the annual monthly anomalies of the NAO, defined as the difference in atmospheric pressure between Lisbon, Portugal, and Reykjavik, Iceland, was obtained from the United States National Oceanic and Atmospheric Administration at https://www.esrl.noaa.gov/psd/data/timeseries/daily/NAO/. Winter (December 1 to March 31) annual mean NAO values were estimated.

Primary production.—Primary production (mg C m⁻³ d⁻¹) data was obtained monthly from the Bermuda Atlantic Time-Series Study (www.batstftp.bios.edu/BATS/production/) station (Figure 1) for the years 1994–2016 (the series has not been updated) at 20-m depth intervals from 1–140 m. The Bermuda Atlantic Time-Series Study station is located in the west-central Sargasso Sea and may be considered representative of conditions affecting leptocephali feeding and migration (Bonhommeau et al. 2008a). Primary productivity averages were estimated from the monthly January 1 to June 30 data at all depths because most primary productivity is produced during this period and it accounts for the transfer time of primary productivity between lower and upper levels of the food chain (Bonhommeau et al. 2008a). Hatching of American Eels occurs about 32–48 h after fertilization (Oliveira and Hable 2010), so the spawning period closely coincides with the early larval period.

Annual mean chlorophyll values (mg/m³) for the Atlantic Continental Shelf extending from Cape Hatteras to the Scotian Shelf between 1997 and 2017 were obtained from https://www.globalchange.gov/browse/indicators/indicator-ocean-chlorophyll-concentrations and based on the following equation: chlorophyll = 0.025867 x year – 51.9279, r² = 0.85, with a mean annual value of 1.14 mg/m³. Chlorophyll values are regarded as a proxy for the amount of photosynthetic phytoplankton present and thus primary productivity.

Gulf Stream velocity.—Florida Current and Gulf Stream velocities and distances between points were estimated for the current center at five points along its length at the intersection of a radial from each continental site to the center of the Gulf Stream (oceanic sites 1–5; Figure 1). The continental sites were the Guana River Dam, Florida (R2) (30.0°N, 81.3°W), Goose Creek, South Carolina (R3), represented by Charleston Harbor, South Carolina (32.7°N, 79.9°W), Cape Hatteras, North Carolina (35.2°N, 75.5°W), due south of Cape Cod, Massachusetts (41.7°N, 70.0°W), and the East River (44.6°N, 64.2°W). Current velocities were daily estimated values from https://www.nws.noaa.gov.polar.ncep.noaa.gov at the “Global RTOFS Z-level Nowcasts/Forecasts” page and were measured weekly between December 18, 2018, and January 15, 2019, and on January 31, 2019. Velocities between two sequential points were the average of the point velocities and used to estimate the travel time (km/d) between those points. Migration distances were also measured from the Gulf Stream to the stream sites (R2–R6 [East River]; Figure 1) used by Wang and Tzeng (1998, 2000), with migration times (days) to shore from the Gulf Stream based on an estimated sustainable glass eel swimming speed of about 5.69 km/d (Wuenschel and Able 2008). The total migration time (days) between the Sargasso Sea spawning area to sites R2–R6 based on otolith measurements (Wang and Tzeng 1998, 2000) were compared with those obtained from the estimated mean spawning time (February 6, range = December 15 to March 20) based on the central 98% of the observations in Figure 4 of Westerberg et al. (2018) and the start of elver stream entrance. This study provides the first breakdown of migration times for each of the three migratory periods experienced by American Eel larval and glass eels—within the Sargasso Sea, within the Gulf Stream, and within oceanic and continental shelf waters between the Gulf Stream and continental streams. Use of the estimated mean spawning time for American Eels of February 6 (Westerberg et al. 2018) adds 39 d to migration periods determined using the Miller et al. (2015) mean spawning date (March 17).

Current speeds affect the timing of larval oceanic migration (Bonhommeau et al. 2008a), but their regional variability and effect on overall migration timing is poorly known, particularly within the Sargasso Sea but also across oceanic and continental shelf waters west of the Gulf Stream. Current meanderings within the Sargasso Sea permit only rough estimates of current velocities between the spawning area and junction with the Florida Current and Gulf Stream. Consequently, the time taken to migrate from the Sargasso Sea spawning area to the Florida Current was estimated from the difference between the total run period between spawning and recruitment and the times to drift between the Gulf Stream sites plus the times to migrate from the Gulf Stream to continental river sites based on a mean sustainable swimming speed for glass eels (Wuenschel and Able 2008) and an assumption of directed swimming (Miller and Tsukamoto 2017).

Statistical analysis.—All annual time series were examined using R (2018) for significant trend and autocorrelation prior to analysis and, if found, removed by first order differencing, which adjusts for first order autocorrelation AR(1) and removes one degree of freedom (Wilkinson et al. 1996).
No smoothing was done because of the shortness of the time series. Linear responses were assumed between biological and environmental variables, but nonlinear responses may also occur (Ottersen et al. 2010). The autocorrelation (acf) function was used to examine correlations (r) within variables at various year-interval lags (Table 2). The Box–Ljung test was used to estimate the statistical significance of autocorrelations within variables, with the minimum number of lags (L) determined by time series length (n), where minimum $L = (10, \sqrt{n})$, with $L = 5$ chosen for the available time series for n ranging from 15 to 24 and significance reported for the largest correlations (https://robjhyndman.com/hints/ljung-box-test). The appropriateness of adjusting for AR(1) autocorrelation, where warranted, was examined by generalized least squares regression with an AR(1) function. Model residuals were normally distributed and the acf and pacf (partial autocorrelation function) plots showed no significant autocorrelation. The cross correlation function (ccf) examined correlations at various year-interval lags between pairs of variables (Table 3). The leading x variable was considered a possible predictor of the y variable, and thus only correlations at negative lags were considered because future values of x should have no effect on current y values. The number of correlation tests (Table 4) was not adjusted by a sequential Bonferroni procedure, which may be inappropriate for ecological data (Moran 2003). Of the 16 correlations in Table 4, the probability of finding 3 significant correlations by chance alone is 0.036.

Correlations were adjusted ($r_{adj}$) for small sample size (<40) when evaluating statistical significance (Zar 1984). The correlation coefficient and coefficient of determination in regression ($r^2$) may be interpreted as effect size measures or magnitudes of effect (Nakagawa and Cuthill 2007; Lakens 2013). Medium and higher effect sizes are perhaps most biologically meaningful, but the importance of an effect size partly depends upon what is studied and the judgment of the researcher (Cohen 1988). Following Jessop (2018)

Benchmark effect sizes were interpreted as follows: r-values of 0.0 to <0.1 as very small, ≥0.1 to <0.3 as small, ≥0.3 to <0.5 as medium, ≥0.5 to <0.7 as large, and ≥0.7 to <0.9 as very large (Kotrlik and Williams 2003). The scales of importance for effect size measures were designed for experimental studies and may be conservative when applied to observational studies. Effect sizes were compared with benchmark values when comparable published effect sizes were unavailable.

A greater understanding of the meaning and interpretation of effect sizes for ecological studies is required.

RESULTS

Fishery Start Relative to Water Temperature

The start of the commercial fishery in the East River was highly correlated with oceanic SSTs between the Gulf Stream, the Scotian Shelf (at the Emerald Basin), and the coastal waters of Mahone Bay (Table 3; Figure 2). Correlations between the fishery start date and offshore water temperatures decreased with increasing distance offshore. Annual SSTs for the seasons examined within the years 1995–2018 increased significantly for sites between the Sargasso Sea and Nova Scotia, except for the Gulf Stream south of Nova Scotia and off Cape Hatteras (Table 5). These exceptions are a consequence of the relatively constant water temperatures during the winter period and increasing annual water temperatures during the remainder of the year because annual SSTs increased significantly at all oceanic sites. For the mean annual increase in SST of the Gulf Stream off Cape Hatteras, the $r_{adj} = 0.91, n = 24, P < 0.001, 95\% CI = 0.81–0.96$, and for the Gulf Stream south of Nova Scotia the $r_{adj} = 0.64, n = 24, P < 0.001, 95\% CI = 0.33–0.83$.

Relationships between Elver Count and Length and Environmental Variables

Annual index counts of American Eel elvers at the East River increased significantly ($r_{adj} = 0.69, n = 17, P = 0.003, 95\% CI = 0.29–0.87$) between 1996 and 2018 (Figure 3; Tables 1 and 2) as did environmental variables such as SSTs

| Variable                                      | Trend     | Autocorrelation | Action   |
|-----------------------------------------------|-----------|-----------------|----------|
| Log10 elver count                             | Increasing| Nonsignificant  | Differenced |
| Elver length                                  | None      | Nonsignificant  | None     |
| Emerald Basin water temperature               | Increasing| Significant     | Differenced |
| Gulf Stream water temperature                 | Increasing| Significant     | Differenced |
| Sargasso Sea water temperature                | Increasing| Significant     | Differenced |
| National Oceanic and Atmospheric Administration NAO | None      | Nonsignificant  | None     |
| Continental shelf chlorophyll                 | Increasing| Significant     | Differenced |
| Sargasso Sea primary productivity             | None      | Nonsignificant  | None     |

TABLE 2. Stationarity (trend) and autocorrelation effects at various lags for the annual time series of environmental variables examined and the action taken in response. Autocorrelation significance was estimated by the Box–Ljung test. See Table 1 for the years of each time series. Statistical significance accepted at $P \leq 0.05$. 
at various sites. Annual elver counts were not significantly correlated with any environmental variable (Table 4). Correlations between the NAO, Sargasso Sea and other oceanic SSTs, and primary productivity with the elver index are most biologically probable at lags of 0 to –2 given that the time between spawning and recruitment is about 1.2 years (this study). The correlation between the elver index and NAO at lag 0 (r_{adj} = 0.31, n = 15, P = 0.27) was significant. The correlation between the elver index and Sargasso Sea SST at lag –4 was nonsignificant (r_{adj} = 0.03, n = 15, P = 0.86) but of large effect size. Water temperatures, such as the Gulf Stream seasonal mean SST, had no significant effect on elver recruitment within a given year (at lag –1; r_{adj} = 0.20, n = 17, P = 0.44; with a small effect size) nor did continental shelf SSTs (at lag –1; r_{adj} = 0.20, n = 17, P = 0.44). As a proxy for primary productivity, chlorophyll values over the continental shelf and in the adjacent ocean northwest of the Gulf Stream (at lag 0; r_{adj} = 0.25, n = 17, P = 0.33; with a small effect size) had no significant effect on glass eel recruitment to the East River.

Elver mean annual lengths varied annually (maximum percent difference = 5.5%) but showed no annual trend (r_{adj} = 0.006, n = 16, P = 0.99) and were not significantly correlated with differences log\_10 elver counts (r_{adj} = 0.20, n = 15, P = 0.48). Elver length was not significantly correlated with the NAO (at lag –2; r_{adj} = 0.47, n = 16, P = 0.057; a medium effect size) or continental shelf chlorophyll concentration (Table 4).

### Relationships between Environmental Variables

Correlations between environmental variables were statistically significant for some variable pairs at zero lag or small negative lags. Thus, Sargasso Sea primary productivity was negatively correlated with the NAO at lag 0 (r_{adj} = –0.59, n = 22, P = 0.003, 95% CI = 0.24–0.81) and chlorophyll concentration decreased with increasing SST over the continental shelf (Emerald Basin) at lag –3 (r_{adj} = –0.48, n = 19, P = 0.039, 95% CI = 0.03–0.76) (Table 4). Although not statistically significant, medium effect sizes occurred for the relationships between the NAO and Sargasso Sea SST at lag 0 (r_{adj} = –0.36, n = 24, P = 0.08), with Emerald Basin SST at lag –1 (r_{adj} = –0.37, n = 24, P = 0.075), and with continental shelf chlorophyll concentration at lag –2 (r_{adj} = 0.35, n = 20, P = 0.13). The time for metamorphosis from leptocephalus to glass eel may be shortest at the latitude of North Carolina (Wang and Tzeng 1998). After entering the Florida Current, leptocephalus travel times to more northerly latitudes are rapid, with about 16 d required to travel between northern Florida and the Gulf Stream at 38.5°N, 64.0°W, which is a common but not the closest approach (mean distance = 730 km; range = 690–765 km) of the Gulf Stream to the East River as it travels northeastward (Table 6). The total time for larval and glass eel migration based on the mean time of spawning of the previous year and the mean time of stream arrival in the next year increased from south to north, from 0.9 years to Florida to about 452 d or 1.2 years to the East River (Table 7). The time for larval American Eels to migrate from the central spawning area to the Florida Current where the Antilles Current joins off South Carolina ranged from 304 to 358 d (Table 7), with a mean of 329 d and a percent difference in values of 10.6%. The percentage of mean total migration time spent exiting the Sargasso Sea was 92–93% for sites from Beaufort Inlet, North Carolina, and south and decreased progressively (81% to 69–70%) northeastward as distances to shore from the Gulf Stream increased. The migration times to each site estimated by Wang and Tzeng (Table 3 in Wang and Tzeng 1998, and 2000) from counts of otolith daily growth rings differed greatly among sites and underestimated migration times based on observed data (Table 7) by a mean of 45.8% (range = 28.4–54.8%), with the smallest percent difference at the Florida site and relatively similar percent differences (range = 45.8–54.8%) north of North Carolina.

### DISCUSSION

**Fishery Start Relative to Water Temperature**

The commercial elver fishery start date at the East River has advanced from about late April to early May in the late 1990s to early April in later years, particularly after 2009, apparently in response to increasing SSTs in

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**TABLE 3. Correlations between the start (day of year) of the commercial elver fishery at the East River and water temperatures (°C) at several distances (km) from the river mouth for the years 1996–2018. Mean water temperatures were measured over periods believed to have substantial elver presence at each site. Longer distances were rounded to the nearest 10 km. The fixed Gulf Stream position for sea surface temperature measurement is due south of Mahone Bay.**

| Site          | Latitude (°N) | Longitude (°W) | Distance | Period       | r_{adj} | 95% CI          | P     | n  |
|---------------|---------------|----------------|----------|--------------|---------|----------------|-------|----|
| Mahone Bay    | 44.40         | 64.10          | 11       | Feb 1 to May 15 | –0.89   | –0.95 to –0.74 | <0.001 | 22 |
| Emerald Basin | 43.90         | 62.90          | 120      | Feb 1 to May 15 | –0.76   | –0.89 to –0.50 | <0.001 | 22 |
| Gulf Stream   | 37.90         | 64.10          | 730      | Dec 1 to Mar 31 | –0.43   | –0.72 to +0.001| 0.047  | 22 |
Mahone Bay, over the central Scotian Shelf at Emerald Basin, and in the northern reaches of the Gulf Stream nearest the central Nova Scotia Atlantic coast. Between 1996 and 2018, the fishery has become earlier by about 22 d. An increase of 1°C in Mahone Bay mean water temperature made the fishery start date earlier by 16 d.

The calendar periods when the highest correlations were found between the fishery start date and SSTs may represent periods of highest glass eel concentrations in the associated oceanic regions. Winter SSTs over the Scotian Shelf have increased above normal for the past decade, with many monthly records broken, notably the high (record since 1985) of February 2017 over the central Scotian Shelf (DFO 2019). Caesar et al. (2018) has linked the extreme warming along the U.S. Northeast Atlantic coast to the Gulf Stream warming, shifting northwards, and moving closer to shore as a consequence of a weakening and slowdown in the Atlantic meridional overturning circulation. The Gulf Stream seasonally shifts northward in autumn and southward in spring, with a north–south variation of about 100 km, possibly reducing the migration distance to shore in northern areas during winter (Frankignoul and de Coëtlogon 2001). Low water temperatures reduce, and high water temperatures enhance, the swimming activity of glass eels (Edeline et al. 2006). Thus, the northward shift in the Gulf Stream and increased SSTs may account for the earlier recruitment of elvers to coastal streams.

**TABLE 4.** Cross correlations between annual (1996–2018, missing 2002–2007) values of the East River elver index and elver length with environmental variables and amongst pairs of environmental variables (differenced as appropriate), with statistical significance ($P \leq 0.05$) estimated for the largest correlations. Lag maximum is five years. The leading environmental variable was considered a possible predictor of the following variable and thus only zero or negative lags were taken as plausible.

| Variable comparison                                                      | Correlations                              |
|-------------------------------------------------------------------------|-------------------------------------------|
| NAO versus log$_{10}$ elver count differenced                           | Nonsignificant at all lags                |
| Sargasso Sea water temperatures differenced versus log$_{10}$ elver count differenced | Nonsignificant at all lags                |
| Gulf Stream water temperatures differenced versus log$_{10}$ elver count differenced | Nonsignificant at all lags                |
| Emerald Basin water temperatures Jan 1 to Apr 30 differenced versus log$_{10}$ elver count differenced | Nonsignificant at all lags                |
| Sargasso Sea primary productivity 0–140 m versus log$_{10}$ elver count differenced | Nonsignificant at all lags                |
| Continental shelf chlorophyll concentration differenced versus log$_{10}$ elver count differenced | Nonsignificant at all lags                |
| Continental shelf chlorophyll concentration differenced versus length   | Nonsignificant at all lags                |
| NAO versus Sargasso Sea water temperatures differenced                  | Nonsignificant at all lags                |
| NAO versus Gulf Stream water temperatures differenced                   | Nonsignificant at all lags                |
| NAO versus Emerald Basin water temperatures differenced                 | Nonsignificant at all lags                |
| NAO versus Emerald Basin Jan 1 to Apr 30 water temperatures differenced | Significant $r_{adj} = 0.44$ at lag $-5$  |
| NAO versus Sargasso Sea primary productivity                            | Significant $r = -0.59$ at lag $0$       |
| NAO versus chlorophyll concentration differenced                         | Nonsignificant at all lags                |
| Sargasso Sea water temperatures differenced versus Sargasso Sea primary productivity | Nonsignificant at all lags                |
| Sargasso Sea water temperatures differenced versus Gulf Stream water temperatures differenced | Nonsignificant at all lags                |
| Emerald Basin water temperatures differenced versus chlorophyll concentration differenced | Significant $r_{adj} = -0.48$ at lag $-3$ |

![FIGURE 2](image-url)  

**FIGURE 2.** Relationship between the annual start of the elver fishery at the East River and mean (February 1 to May 15) water temperatures in Mahone Bay between 1996 and 2018 (excluding 2000). The use of the raw data uncorrected for significant trend in each variable inflates the $r_{adj}^2$ from 0.716 (differenced) to 0.779 (raw data), a percent difference of 8.45%.
The significant increase in elver recruitment to the East River after about 2011 and the increase in yellow eel recruitment to the Moses–Saunders Dam on the upper St. Lawrence River from 994 American Eels in 2001 to about 51,200 American Eels in 2011 and 2012 (Cairns et al. 2014) may be signs that oceanic conditions are currently favoring higher recruitment. However, increased recruitment of American Eels to continental waters may not result in increased juvenile abundance in Nova Scotia streams, depending on the nature of the riverine habitat (Bowlby 2018). The relationship between elver recruitment and silver eel production has yet to be adequately investigated (Harrison et al. 2014). Elver mortality is also very high during the first months after continental arrival (Jes sop 2000), with probable density-dependent mortality (DFO 2014; Shepard 2015). Increased recruitment to an area in the northern part of the range of American Eels may not apply elsewhere. Regional differences occur in the timing, continental distribution, and recruitment of

### TABLE 5
Significance of the correlations (1995–2018) between sea surface temperature (°C) and year for sites from Nova Scotia to the Sargasso Sea for the seasonal time periods indicated. The “Gulf Stream, Nova Scotia” site is due south of Mahone Bay and the “Gulf Stream, Cape Cod” site is due south of Cape Cod.

| Site                              | Latitude (°N) | Longitude (°W) | Period          | $r_{adj}$ | 95% CI          | P    | n  |
|-----------------------------------|---------------|----------------|-----------------|----------|-----------------|------|----|
| Mahone Bay                        | 44.40         | 64.10          | Feb 1 to May 15 | 0.57     | 0.23–0.79        | 0.003| 24 |
| Emerald Basin                     | 43.90         | 62.90          | Jan 1 to Apr 30 | 0.67     | 0.36–0.84        | <0.001| 24 |
| Gulf Stream, Nova Scotia          | 37.90         | 64.10          | Dec 1 to Mar 31 | 0.33     | -0.08 to +0.65  | 0.11 | 24 |
| Gulf Stream, Cape Cod             | 37.40         | 70.00          | Jan 1 to May 15 | 0.67     | 0.36–0.84        | <0.001| 24 |
| Gulf Stream, Cape Hatteras        | 35.9          | 74.1           | Jan 1 to May 15 | 0.38     | -0.03 to +0.68  | 0.067| 24 |
| Gulf Stream, South Carolina       | 31.99         | 79.01          | Dec 1 to Apr 15 | 0.74     | 0.49–0.88        | <0.001| 24 |
| Sargasso Sea                      |               |                | Dec 15 to Mar 20| 0.60     | 0.26–0.81        | 0.002| 24 |

### TABLE 6
Florida Current and Gulf Stream grand mean current velocities between Florida and Nova Scotia at midcurrent locations offshore by site, distance travelled, and travel time between sites.

| Site and total | Distance between sites (km) | Velocity (m/s) | Travel time (d) |
|----------------|-----------------------------|----------------|-----------------|
| Guana River, Florida | 0 | 1.36             |                |
| Goose Creek, South Carolina | 228 | 1.36 | 117.3 | 1.95        |
| Cape Hatteras, North Carolina | 583 | 1.41 | 117.4 | 5.03        |
| Cape Cod, Massachusetts | 525 | 1.43 | 120.4 | 4.39        |
| East River, Chester, Nova Scotia | 588 | 1.53 | 125.2 | 4.76        |
| Total | 1,924 | 16.13 |

*Gulf Stream due south of Cape Cod on longitude 70.0°W.

*Gulf Stream due south of the East River on longitude 64.0°W.

**FIGURE 3.** Graphs of the annual values for (A) the American Eel elver index at the East River, (B) Sargasso Sea mean water temperatures for the December 15 to March 20 spawning period, and (C) Emerald Basin mean water temperatures between February 1 and May 31, when glass eels are believed to be moving shoreward.

**TABLE 6.** Florida Current and Gulf Stream grand mean current velocities between Florida and Nova Scotia at midcurrent locations offshore by site, distance travelled, and travel time between sites.
elvers within Atlantic coastal Canada (Jessop 1998) and along the Atlantic coast of the USA (Sullivan et al. 2006; Shepard 2015). Glass eel and elver recruitment surveys in Atlantic coast states have varied widely in index values among years and sites but within sites have generally shown no trend (Shepard 2015). In northern Europe, glass eel recruitment has declined by more than 95% since the 1980s (Westerberg et al. 2018) but has recently (2011) reversed its long decline and remains low (ICES 2019). In southern Europe (Portugal), no trend in European Eel recruitment has been detected in the Minha River estuary (Correia et al. 2018), supporting the hypothesis of regional differences in recruitment.

The absence of significant correlations between the East River elver index and Sargasso Sea primary productivity and water temperatures may reflect small sample size rather than a true failure to support the hypothesis that larval survival and elver recruitment is substantially controlled by food availability, which is influenced by water temperature, in the months after hatching, as proposed by Knights (2003) for the European Eel and as supported by Bonhommeau et al. (2008a, 2008b) and Arribas et al. (2012). Food limitation effects on larval survival probably most affect the youngest, smallest larvae that have not yet accumulated energy reserves from successful feeding that could limit the effect of short-term food scarcity (Miller et al. 2016; Miller and Tsukamoto 2017). The absence of significant correlations between the East River elver index and other environmental variables, although effect sizes were often medium to large, may be due to low sample sizes. In contrast, the glass eel index for American Eels (Little Egg Inlet, New Jersey, and Beaufort Inlet, North Carolina) was significantly correlated with Sargasso Sea primary productivity (r = 0.71, n = 11) and negatively correlated with increasing water temperatures (r = –0.87) as was a European Eel index (r = 0.74, n = 13 and r = –0.88, respectively) (Bonhommeau et al. 2008a) despite low sample sizes, indicating that correlations of very large effect size may be significant at small sample sizes. European Eel recruitment to the Loire River was significantly correlated with Sargasso Sea primary productivity (r = 0.81, n = 10), although no significant relationship was found for six other recruitment indices (Bonhommeau et al. 2008b). Correlations of medium effect size might be biologically interesting but require a time series length of 20–40 years to become statistically significant.

The short East River elver index time series and the high (35%) proportion of missing values (years 2002–2007) may result in biased parameter estimation, reduced generalizability of results, lower statistical power, and higher standard errors given that most statistical procedures prefer complete data sets (Dong and Peng 2013). Significant

| Site                        | Total migration period (d) | Distance from GS to shore (km) | Travel time to shore (d) | Travel time between GS sites (d) | Travel time spawning area to GS (d) | Percent difference between observed and otolith migration periods |
|-----------------------------|----------------------------|--------------------------------|--------------------------|---------------------------------|-----------------------------------|---------------------------------------------------------------|
| Guana River, Florida (R2)   | 330                        | 138                            | 24                       | 2                               | 265                               | 28.4                                                          |
| Goose Creek, South Carolina | 372                        | 158                            | 28                       | 0                               | 305                               |                                                                |
| Beaufort Inlet, North Carolina (R3) | 364                        | 124                            | 22                       | 3                               | 300                               | 49.1                                                          |
| Annaquatucket River, Rhode Island (R4) | 442                        | 448                            | 79                       | 6                               | 319                               | 54.8                                                          |
| East River, Chester, Nova Scotia (R6) | 452                        | 730                            | 128                      | 6                               | 279                               | 45.8                                                          |
| Musquash River, New Brunswick (R5) | 450                        | 754                            | 132                      | 6                               | 272                               | 49.2                                                          |

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TABLE 7. American Eel elver total observed migration period (mean spawning date to mean elver stream migration start), mean distance between the center of the Florida Current and Gulf Stream (GS) and continental sites (R2–R6) used by Wang and Tzeng (1998), mean migration times between the center of the current and the shore at each site estimated assuming a glass eel mean directed and sustained swimming speed of 5.69 km/d (Wuenschel and Able 2008), travel time in the Gulf Stream between Goose Creek, South Carolina, and other sites given that most eel larvae enter the Florida Current near 33°N (Kleckner and McCleave 1982), travel time between the spawning area and Gulf Stream estimated as the difference between the total migration period and travel times between Gulf Stream sites and from Gulf Stream sites to shore sites, and percent difference between observed oceanic migration durations and those calculated from otolith daily ring counts (Table 3 in Wang and Tzeng 1998).
correlations reported between the elver indices of European Eels and the NAO vary in sign, negative \( r = -0.35, n = 66 \) at lag 1, and \( r = -0.43 \) at lag 8\) by Friedland et al. (2007) and positive \( r = 0.72, n = 9 \) by Arribas et al. (2012).

The conditions affecting elver length may have little effect on elver recruitment given the absence of a relationship between elver mean annual lengths and elver recruitment and the absence of significant correlations between these variables with continental shelf chlorophyll concentration. Food availability over the continental shelf, as represented by chlorophyll concentration, has little influence on the regulation of glass eel length after larval metamorphosis and at initial recruitment because glass eels do not feed while crossing the continental shelf (Boëtius and Boëtius 1989; Bureau du Colombier et al. 2008). Annual mean lengths and weights did not decline in the East River although Sullivan et al. (2006) reported declines in annual mean lengths from streams in New Jersey and North Carolina. The time series lengths for these sites were similar \( (n = 15–17) \) but the study periods differed \( (1996–2018 \) for East River, \( 1989–2004 \) for New Jersey, and \( 1987–2003 \) for North Carolina). European Eel elvers have declined in annual mean length and weight since the 1960s, a decline that has been linked to the decline in glass eel recruitment (Désaunay and Guerault 1997).

The NAO, which is strongest in winter, influences juvenile American Eel recruitment in several ways, including by affecting primary productivity and larval food supply in the Sargasso Sea (Bonhommeau et al. 2008a, 2008b; Arribas et al. 2012), the strength and path of the Gulf Stream and North Atlantic Current that transport larvae and glass eels to continental shores (Knights 2003; Hurrell and Deser 2010), and changes in the position and characteristics of the ocean salinity and temperature front marking the northern boundary of the Sargasso Sea spawning area (Castonguay et al. 1994; Friedland et al. 2007). The negative correlation between the NAO and Sargasso Sea primary productivity noted here was also reported by Steinberg et al. (2012), while the NAO and zooplankton production in the Sargasso Sea are negatively correlated \( (Saba et al. 2010) \). Sargasso Sea primary productivity is a major factor in food production for larval American Eels given the strong linear relationship between phytoplankton and particulate organic matter, called marine snow and consisting of zooplankton fecal pellets and larvacean houses, which is considered a source of food for larval American Eels (Otake et al. 1993; Mochioka and Iwamizu 1996; DuRand et al. 2001; Steinberg et al. 2012). Increased zooplankton production is largely driven by increased phytoplankton production and may provide increased food for larval American Eels in the form of particulate organic matter. Mesozooplankton \( (>200 \mu m) \) production in the Sargasso Sea is highest during February through April (Steinberg et al. 2012), coincident with the American Eel spawning season. Ayala et al. (2018) found that European Eel leptocephali often consume gelatinous hydrozoa plankton materials.

Although primary productivity and SST in the Sargasso Sea are typically negatively related (Bonhommeau et al. 2008a, 2008b), this study found no similar relationship, which may help explain the increased American Eel elver recruitment during a period of increasing Sargasso Sea SST. Zooplankton production and Sargasso Sea SST were positively correlated, with a weaker positive relationship between zooplankton biomass and primary productivity (Steinberg et al. 2012). However, over the continental shelf and in the ocean northwest of the Gulf Stream, the primary productivity proxy chlorophyll-a concentration was negatively correlated with SST, largely due to the higher productivity associated with the cooler waters over the continental shelf and in the ocean northwest of the Gulf Stream and the lower productivity of the warm waters of the Sargasso Sea (Reul et al. 2014). The interlinked variability in the NAO and primary productivity and its proxies Sargasso Sea SST and chlorophyll-a concentration may influence early larval survival and subsequent glass eel recruitment to continental shores by regulating food production, with low food availability resulting in density-dependent mortality and reductions in the subsequent recruitment of glass eels (Knights 2003; Miller et al. 2016). Primary production over the continental shelf and in oceanic waters northwest of the Gulf Stream may not directly affect glass eel survival because glass eels do not feed while crossing the continental shelf and survive on energetic reserves until resuming feeding at estuarine arrival and beginning pigmentation (Tesch 1977; Boëtius and Boëtius 1989; Bureau du Colombier et al. 2008).

**Larval and Glass Eel Migration Times**

Larval oceanic migration may occur by passive drift with oceanic currents and by directed larval swimming depending upon the stage of migration, larval growth, and timing of metamorphosis (Rypina et al. 2014; Miller et al. 2015; Naisbett-Jones et al. 2017). Migration times to larval metamorphosis and the total migration time from hatching to continental arrival have been estimated from counts of the daily rings in otoliths (Wang and Tseng 1998; Arai et al. 2000; Powles and Warlen 2002) and from the hatching dates of newly hatched leptocephali to continental arrival (McClean 2008; Bonhommeau et al. 2010), which is analogous to the duration between the mean spawning period and continental arrival used in this study. Counts of otolith daily rings may underestimate true ages of American Eel glass eels, with the bias increasing northward as the distance of the Gulf Stream increases from shore, thereby underestimating migration duration to the East River by a third or more (45.8%) relative to other
methods (Figure 2 in Bonhommeau et al. 2010; this study). Accurate estimates of oceanic migration times are important to understanding basic American Eel life history, for guiding the development of particle tracking models, and for evaluating the degree of effect by environmental conditions on the stages of oceanic migration, amongst other reasons. A given environmental effect may apply differently to different migration stages, and stage duration may influence the application of the environmental effect.

The duration of low water temperatures experienced by glass eels during shoreward migration offers one explanation for the disparity between otolith-derived and observed migration durations. Daily ring deposition in glass eel and elver otoliths ceases at water temperatures ≤10°C for Japanese Eels Anguilla japonica (Fukuda et al. 2009) and may do so for American Eels. Glass eel otolith increments and otolith radius are not proportional to body length, thereby underestimating the true age of American Eels (Cieri and McCleave 2000). South of Cape Hatteras, between December and March of 2018–2019 during which time glass eels recruit to coastal streams, water temperatures across the continental shelf remained above 10°C, except during much of January when temperatures were about 8°C in a narrow coastal band. Transit times between the Gulf Stream and coast increase greatly with increasing latitude north of Cape Hatteras as does the proportion of water temperatures <10°C. North of Cape Hatteras, daily water temperatures between January 1 and April 30 were ≤5°C for about 19% of the distance between the Gulf Stream and the East River along the 155° radial (closest mean approach of the Gulf Stream) and ≤10°C for 24% of the distance. The distance between the Gulf Stream and the East River averaged 529 km (range 421–708 km) due to the presence of warm-core rings much of the time. Water temperatures in Mahone Bay did not exceed 10°C before early to mid-June, with the last pigment stage 1 glass eels (Haro and Krueger 1998) entering the East River between early May and early June. If the estimated migration time between the Gulf Stream and the East River is 99 d and if 24% of that time (19 d) shows no otolith growth, then adding that time to the migration time of 72 d beween metamorphosis and shore estimated from otolith analysis (Wang and Tzeng 1998), the resultant migration time of 89 d is close to the nonolith estimate of 93 d based on a migration speed of 5.69 km/d (Wuenschel et al. 2008). This is consistent with the negative effect of low water temperatures on otolith daily ring formation.

Westerberg et al. (2018) concluded from surface current models that most leptocephali of both European Eels and American Eels are retained within the Sargasso Sea south of the Subtropical Frontal Zone for as much as a year and may die there, with few escaping to the Florida Current and Gulf Stream. An alternative explanation is that the larval sampling surveys were too late and in the wrong position to detect the center of the spawning activity, but it is unclear where an alternative core spawning area might be. The models do not account for the possibility of directed, active swimming within the Sargasso Sea towards the Gulf Stream by larval American Eels, as hypothesized by Miller et al. (2015) and Naisbett-Jones et al. (2017). Permitting active swimming in a northwest direction in a particle tracking model resulted in a high success rate for escaping the Sargasso Sea and reaching continental waters (Rypina et al. 2014). A very low larval escapement from the Sargasso Sea seems inconsistent with reported elver fishery catches averaging 3,564 kg (range = 765–8,553 kg) between 1994 and 2017 in Maine (G. Wipfelhauser, Department of Marine Resources, personal communication) and 2,369 kg (range = 480–4,420 kg) in Atlantic Canada between 1990 and 2011 (Cairns et al. 2014).

Current patterns in the Sargasso Sea consist of a general westward drift consisting of approximately equal numbers of complex cyclonic and anticyclonic eddies with low current velocities (Luce and Rossby 2008). Near-surface waters of the Sargasso Sea mostly flow southwest between Bermuda and the Gulf Stream, with current velocities of about 0.9 km/d near Bermuda and 5.2 km/d near the Gulf Stream (Rossby et al. 2005). Current meandering results in a migration route much longer than a direct route (Munk et al. 2010) and may account for the high proportion of migration time spent transiting the Sargasso Sea.

American Eel larvae may transit from the Sargasso Sea to the Florida Current substantially via the northwest-flowing Antilles Current, which is not clearly defined throughout the year, occurs largely during winter (McCleave 1993; Kleckner and McCleave 1985; Miller et al. 2015), and joins the Florida Current between about 30°N and 33°N. At the northern limit approximately off Cape Romaine, South Carolina, American Eel larval abundance was about six times greater than off southern Florida, increasing to about nine times greater at Cape Hatteras (Kleckner and McCleave 1982). American Eel larvae metamorphose over a period of 18–41 d (Arai et al. 2000), a period within that estimated for the transition from the Gulf Stream to continental streams south of Cape Hatteras. Between Cape Hatteras and the Scotian Shelf, American Eel leptocephali presumably metamorphose mostly in oceanic waters outside the continental shelf, with glass eels crossing the continental shelf (Tesch 1977; Kleckner and McCleave 1985; Wuenschel and Able 2008; Miller et al. 2015).

American Eel (this study) and European Eel (Bonhommeau et al. 2008a, 2008b) glass eel recruitment indices have some similarities in their responses to oceanic
environmental conditions because both migrations can be considered a dispersal-mortality problem (McCleave 1993). However, temporal and geographic trends in glass eel recruitment appear to differ between European Eels (sharp decrease over a wide geographic area [Westerberg et al. 2018], perhaps excepting the southernmost European estuary [Arribas et al. 2012]) and American Eels (sharp decrease in yellow eel recruitment to the upper St. Lawrence River or increase in yellow eel abundance and elver recruitment in Atlantic Canada [DFO 2014; this study]). In this study, American Eel elver index relationships with environmental variables were not statistically significant, although with medium effect sizes, while comparable relationships were found significant for European Eel elver indices having longer time series. Longer time series for American Eel elver indices are clearly needed for a better understanding of the relationships between elver indices and oceanic environmental conditions. The increasing SSTs over the past decade in the northwestern Atlantic Continental Shelf waters and Gulf Stream have produced earlier elver recruitment to the East River and presumably other northeastern Atlantic coastal streams. Otolith-based estimates of the duration of various migratory stages were again shown to be much shorter than those derived from observed run time data, and the usefulness of otolith-based total migratory period estimates is questionable (McCleave 2008; Bonhommeau et al. 2010; this study). The hypothesis that elver recruitment indices may not be predictive of stream juvenile abundance and silver eel escapement also requires further study.

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