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Patterns in longitudinal distribution of American Eel (*Anguilla rostrata*) population characteristics in rivers of Puerto Rico

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Abstract

American Eel (*Anguilla rostrata*) population characteristics and distribution remain drastically understudied in the Caribbean region. We conducted the first island-wide study to evaluate the distribution of density, length, and sex in relation to distance from the mouth of 23 stream reaches in five rivers in Puerto Rico. We found 287 American Eel at a mean density of 156.7 fish/ha. Sex ratios favored females (52:3) but most of the eel sampled were undifferentiated or undetermined. Generalized linear modeling indicated that upstream habitats with low eel density were optimal environments for production of large and female eel. Our findings indicate that Puerto Rico could significantly contribute to the spawning population and strengthen knowledge of American Eel in the Caribbean. Our findings could be used to guide local and range-wide conservation efforts to ensure stream connectivity and access to optimal upstream habitat for survival of the population.

KEYWORDS

Anguilla rostrata, Caribbean, dams, population characteristics, rivers, sex determination

Abstracto

Las características y distribución de la Anguila Americana (*Anguilla rostrata*) son poco estudiadas en el Caribe. Realizamos el primer estudio a nivel isla para evaluar la distribución de la densidad, el largo y el sexo de anguilas con relación a la distancia a la desembocadura del río en Puerto Rico. Muestreamos 23 secciones de río en gradientes longitudinales en cinco ríos. Encontramos 287 anguilas con una densidad promedio de 156.7 peces/ha. Las proporciones de sexo favorecieron a las hembras (52:3) y la muestra fue mayormente indiferenciada o indeterminada. Modelos lineales generalizados indican que los hábitats río arriba, con baja densidad de anguilas, son óptimos para la producción de hembras grandes. Esto indica que Puerto Rico podría contribuir significativamente a la población reproductiva, fortaleciendo el conocimiento general en el Caribe. Estos hallazgos pueden guiar la conservación local

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y a través de toda su distribución para garantizar la conectividad de ríos y el acceso a hábitats río arriba para la supervivencia de la población.

1 | INTRODUCTION

The American Eel (*Anguilla rostrata*) is a widespread, facultatively catadromous fish with a complex and enigmatic life history. The American Eel distribution extends from southeastern Greenland to Northeastern Venezuela, including Central America, the Gulf of Mexico, and the Caribbean (Benchetrit & McCleave, 2016). Despite the extremely broad distribution, this species exists as a single, panmictic population that spawns in a single location, the Sargasso Sea of the Atlantic Ocean (Benchetrit & McCleave, 2016). Adult American Eel die after reproduction and the larvae, known as leptocephali, are carried by ocean currents to diverse estuarine and freshwater environments (Benchetrit & McCleave, 2016; Haro et al., 2000; McCleave & Kleckner, 1987; Tsukamoto et al., 1998). Leptocephali metamorphose into sexually undifferentiated glass eel during migration into estuaries, where they subsequently develop into elver and yellow eel (McCleave & Kleckner, 1982; Oliveira & McCleave, 2000). They can reside in freshwater, saltwater, and brackish environments until reaching sexual maturity as silver eel, when they begin their extensive migration to the Sargasso Sea to spawn and complete their life cycle (Lamson et al., 2006; McCleave & Edeline, 2009; Tesch & Thorpe, 2003; Thibault et al., 2007; Tsukamoto et al., 1998). The American Eel's ability to occupy varied habitats and their widespread dispersal has posed challenges to identifying distribution patterns in continental waters throughout its range.

Throughout its broad range, American Eel are an ecologically, culturally, economically valuable, and highly threatened species (ASMFC, 2017; Davis et al., 2004). Eel are a predator in freshwater habitats and prey for many species in both marine and freshwater habitats (Béguer-Pon et al., 2012; Engman et al., 2017; Helfman & Clark, 1986; Thompson et al., 2005). American Eel are also a valuable economic and cultural fisheries resource. American Eel are harvested at all life stages by many indigenous tribes and other peoples in subsistence and recreational fisheries throughout its native range (Arai, 2014; ASMFC, 2017; Davis et al., 2004). Commercial harvest of American Eel is largely focused on glass eel, which are primarily exported to Asian countries for rearing in aquaculture to adults (ASMFC, 2017; COSEWIC, 2012; MacGregor et al., 2008). Despite their value, American Eel are imperiled and face many threats, such as instream barriers, pollutants, climate change, environmental impacts, and parasitic diseases (Buttermore et al., 2018; Hein et al., 2014; Jessop & Lee, 2016; Kwak et al., 2016). These threats have been linked to declines in abundance and subsequent extinction risk (ASMFC, 2017; COSEWIC, 2012; Jacoby et al., 2017), which has led to its listing as endangered by the International Union for Conservation of Nature Red List of Threatened Species (Jacoby et al., 2017). Despite these known risks, species assessments in North America determined that the species did not warrant protection (Shepard, 2015). Range-wide assessments are needed to understand overall trends and conservation needs of the species (Cairns et al., 2022), but there are knowledge gaps from southern parts of its distribution.

Studies from temperate regions indicate trends in size, sex, and density distributions along estuaries, rivers, and latitudinal gradients in the American Eel population (Goodwin & Angermeier, 2003; Jessop, 2010). Most commonly, abundance and density decrease inland compared to environments closer to the ocean, especially in dammed rivers (Camhi et al., 2021; Goodwin & Angermeier, 2003; Smogor et al., 1995; Wiley et al., 2004). Low proportions of females occur in downstream and brackish water environments, which are characterized by high American Eel densities and overcrowding (Krueger & Oliveira, 1999) whereas, upstream freshwater environments harbor predominantly female eel, which are typically longer and heavier than males (Bonvechio et al., 2018; Goodwin & Angermeier, 2003; Hansen & Eversole, 1984; Helfman et al., 1984; Morrison & Secor, 2003). Larger size in upstream and freshwater habitats may be related to low densities that may result in less competition and higher food availability (Goodwin & Angermeier, 2003; Krueger & Oliveira, 1999; Oliveira, 1999; Smogor et al., 1995; Vélez-Espino & Koops, 2010; Wiley et al., 2004). Body size and proportion of female American Eel also increase with latitude (Jessop, 2010; Vélez-Espino & Koops, 2010). Although these trends have been documented in the northern range, American Eel in the southern range may not exhibit similar trends. Resolving the spatial distribution of population characteristics (i.e., population density, body length, and sex) throughout this species' broad distribution is essential for management and conservation of the species, because of effects of local anthropogenic impacts and relative reproductive contributions to the entire population.

The status and ecology of American Eel in the Caribbean, Central America, and South America is largely unknown. Commercial fisheries occur in several locations throughout the Caribbean and South America, but are not well-quantified (ASMFC, 2017; Benchetrit & McCleave, 2016; CITES, 2018). Recent descriptions of American Eel populations in the Caribbean described the species as widespread in Puerto Rico and predominantly threatened by instream barriers and habitat loss (Cooney & Kwak, 2013; Kwak et al., 2013, 2019; Roghair et al., 2014). Island-wide surveys indicated that large and female eel occurred in Puerto Rico and that lower densities may have occurred in upstream environments (Kwak et al., 2019).

Our goal was to determine if density, length, and sex of American Eel vary across riverine longitudinal gradients (i.e., headwaters to downstream sections) in patterns similar to what has been observed in temperate regions. To date, longitudinal patterns of American Eel population structure in streams outside of the continental United States and Canada have not been documented. Thus, extensive knowledge gaps exist in the southern portion of the American Eel's range, including the entire Caribbean region. Puerto Rico is an ideal system to address these knowledge gaps for multiple reasons. As the easternmost island of the Great Antilles, Puerto Rico is centrally located in the Caribbean and directly South of the Sargasso Sea and the island's rivers and streams are broadly representative of the entire Caribbean region. Therefore, research in Puerto Rico will provide critical knowledge on the reproductive potential and contributions of southern portions of the population, and those located at shorter distances from the spawning location. Puerto Rico's scale is another reason that it is an ideal study system, with more than 50 rivers, all of which are less than 100 km from the headwaters to the river mouth. This compact scale and accessibility of rivers due to a dense road network make sampling across the entirety of a river system and studies involving multiple rivers feasible in Puerto Rico.

2 | METHODS

2.1 | Study design

American Eel were collected from November 2020 to January 2021 (dry season) and from June to August in 2021 (wet season). The five river basins sampled, Río Piedras, Río Mameyes, Río Sabana, Río Matilde, and Río Guanajibo, were located in northern, northeastern, southern, and western regions of Puerto Rico (Figure 1). Rivers were selected based on a lack of in-stream barriers to migration, accessibility for eel (Cooney & Kwak, 2013), and known occurrence of American Eel (Kwak et al., 2019; Roghair et al., 2014). The Río Piedras was selected to evaluate implications of urbanization on American Eel distributional patterns.

Four to six sampling locations were selected on the mainstem river or tributaries of each river basin, distributed from upstream to downstream environments (Figure 1; Table 1). Twenty-three sites across all basins were sampled from November 2020 to January 2021 (i.e., during Puerto Rico's dry season) and 14 sites in the Río Piedras, Río Mameyes, and Río Matilde were resampled from June to August (wet season) in 2021. All sites could not be resampled in the wet season due to high river flows, which would yield unrepresentative samples. American Eel were sampled using pulsed direct current backpack electrofishing, employing a 3-pass removal technique to estimate American Eel density at each site. A 60-m long stream reach was measured and blocked by nets on each end. Upstream block nets were not placed on reaches with natural in-stream barriers or locations of high-water velocity that would impede escapement from

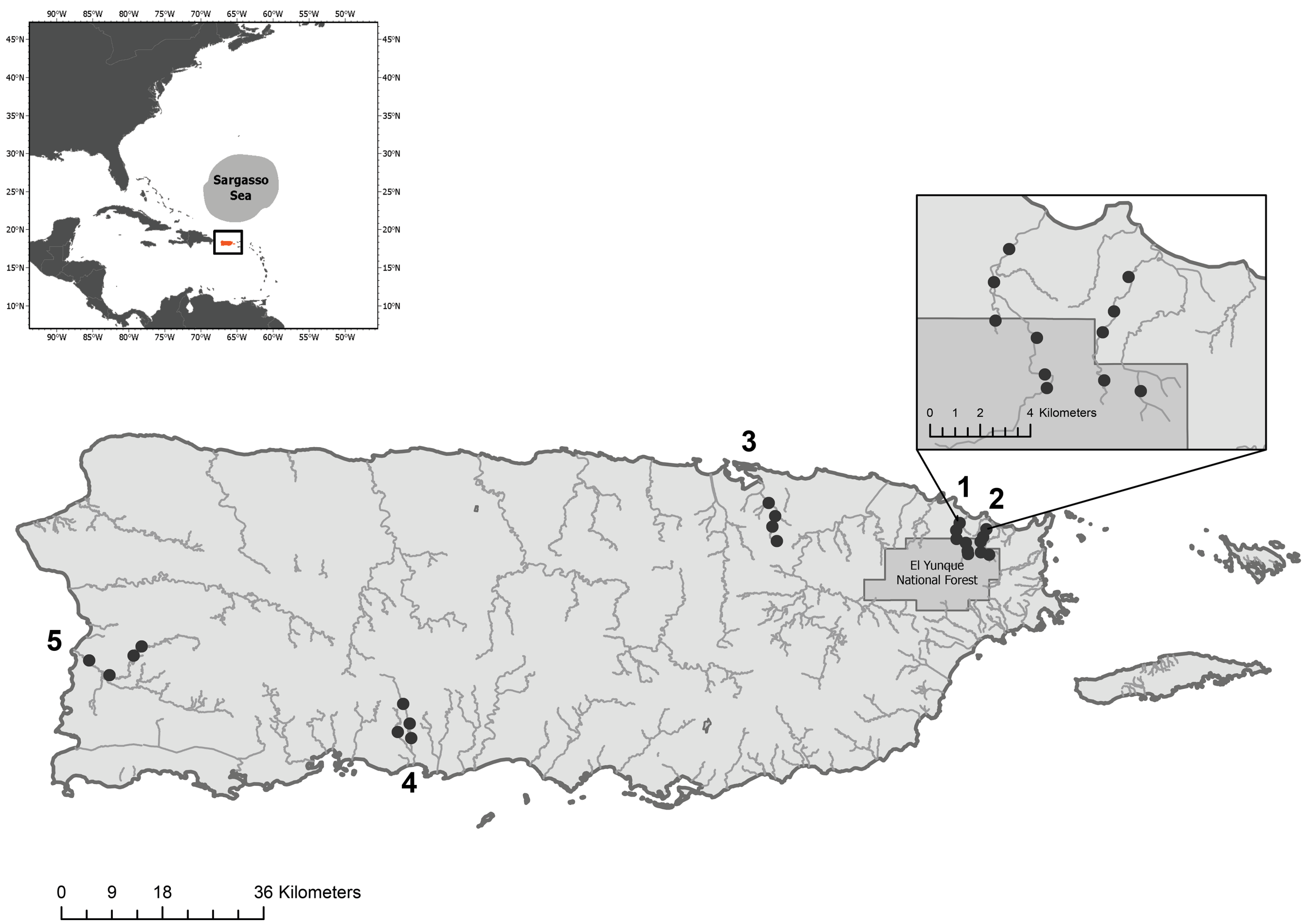

FIGURE 1 Map of American Eel sampling reaches ($n=23$) located in five river basins throughout the north, south, east, and west of the island of Puerto Rico during the dry (November 2020–January 2021) and wet sampling seasons (June 2021–August 2021) seasons. (1) Río Mameyes, (2) Río Sabana, (3) Río Piedras, (4) Río Matilde, (5) Río Guanajibo. All sites were sampled using a pulsed-DC electroshocking method on 60-m long reaches.

TABLE 1 American Eel sampling site coordinates and distances from the river mouth within five river basins located in the north, south, east, and west of the island of Puerto Rico. Sampling was conducted at 23 sites using a 3-pass pulsed-DC electrofishing method during the dry season (November 2020–January 2021) and 14 sites were resampled during the wet season (June 2021–August 2021).

Site ID	Stream	River basin	Distance from river mouth (km)	Latitude (N)	Longitude (W)	Sampling	
						Dry season 2020–2021	Wet season 2021
46C	Río Piedras	Río Piedras	4.75	18.4053657	−66.0690448	X	X
46A	Río Piedras	Río Piedras	8.61	18.3840681	−66.0586831	X	X
46B	Río Piedras	Río Piedras	11.2	18.3670476	−66.0631768	X	X
RP2	Río Piedras	Río Piedras	14.9	18.343722	−66.0560056	X	X
4Q	Río Mameyes	Río Mameyes	2.22	18.3730357	−65.7635835	X	X
4K	Tabonuco	Río Mameyes	3.97	18.361063	−65.769013	X	X
RM2	Tabonuco	Río Mamayes	5.89	18.347116	−65.7684802	X	X
4I	Río Mameyes	Río Mameyes	7.02	18.3408842	−65.7536526	X	X
4F	Río Mameyes	Río Mameyes	9.15	18.3276234	−65.7507864	X	X
4D	Río Mameyes	Río Mameyes	9.78	18.3226959	−65.7500712	X	X
5C	Río Sabana	Río Sabana	2.48	18.362925	−65.7208063	X	
5A	Río Sabana	Río Sabana	4.32	18.350457	−65.7260138	X	
RS5	Río Sabana	Río Sabana	5.35	18.3428929	−65.7300596	X	
5D	Río Sabana	Río Sabana	7.69	18.3254706	−65.7295268	X	
RS4	Río Pitahaya	Río Sabana	9.72	18.321595	−65.7164504	X	
28D	Río Canas	Río Matilde	5.5	18.0249	−66.6409652	X	X
28E	Río Pastillo	Río Matilde	7.49	18.0347752	−66.6624655	X	X
28C	Río Canas	Río Matilde	7.84	18.0400361	−66.6447425	X	X
28B	Río Canas	Río Matilde	14.0	18.0802422	−66.6538603	X	X
RG3	Río Hondo	Río Guanajibo	4.71	18.1604514	−67.1497042	X	
35H	Río Rosario	Río Guanajibo	10.4	18.1267652	−67.1237605	X	
35B	Río Rosario	Río Guanajibo	14.1	18.1583217	−67.085124	X	
RG2	Río Rosario	Río Guanajibo	16.9	18.1732659	−67.0722671	X	

the reach. Additionally, reach length, mean stream width, discharge, and distance from the river mouth were measured at each sampling reach. Density at each sampling site was estimated from population size estimates using the Carle-Strub depletion method and reach area measurements. The Carle-Strub method (via the FSA package in R) used a maximum weighted likelihood estimation method (Carle & Strub, 1978; Hedger et al., 2013; Ogle, 2016). American Eel density at each site was estimated by dividing population size by the respective area of the reach.

Biological traits were measured on each American Eel and sex was determined by gonad examination for sacrificed individuals from each site. Body length (mm), wet weight (g), and life stage were recorded for all collected eel. Individuals were sacrificed for sex determination using a solution of MS-222, following IACUC protocol 20–216. All eel with body length ≥200 mm were sacrificed for gonad examination. Some eel with body length <200 mm were released at sampling sites and were assumed to be undifferentiated (Goodwin & Angermeier, 2003; Krueger & Oliveira, 1999; Machut et al., 2007).

2.2 | Gonad examinations

Sacrificed American Eel were transferred to the laboratory facility at North Carolina State University for sex determination. Gonadal tissue were dissected and macroscopically identified to determine if eel were female, male, undifferentiated, or undetermined (Tesch & Thorpe, 2003). Whenever macroscopic identification was not possible, the gonad squash technique was applied by extracting and staining a piece of gonad tissue with an aceto-carmine solution, pressing it between two microscope slides, and viewing the tissue sample through a compound microscope to identify presence and absence of oocytes or spermatogonia following descriptions from Guerrero and Shelton (1974). If the incomplete tissue was not differentiated via the gonad squash technique, or if gonad tissue was not detected, eel of body length <200 mm were assumed to be undifferentiated and eel with body length ≥200 mm were assumed to be undetermined. These two categories accounted for misidentification resulting from the gonad examination techniques used in the study.

2.3 | Models of American Eel density and body length

Linear regression models were used to assess how American Eel density and body length, both continuous variables, were influenced by geographic and temporal variables in Puerto Rico river basins. Model assumptions were tested for linearity, normality, and homogeneity. Density and body length models were fit as functions of river basin, distance from river mouth, season, the interaction between distance from the river mouth and river basin, and density (only for the body length model). The continuous covariate, distance from the river mouth, was scaled by subtracting the mean and dividing by the standard deviation prior to fitting candidate models. All subsets of global models were explored to identify the best fitting model. Prior to model fitting, spearman correlation values and variance inflation factors were calculated for all covariates and for the global body length model to control for collinearity.

To select the best model that explained variation in density of American Eel, all candidate models were ranked using Akaike Information Criterion, corrected for small sample sizes ($AICc_i$), delta-AICc (Δ_i (AICc)) and weighted AICc (w_i (AICc; Burnham & Anderson, 2004)). The 95% confidence set of linear regression models was calculated with cumulative AICci weight ≥0.95 (Burnham & Anderson, 2002) and R^2 values were used to evaluate the predictive ability of the top model and competitive models. Statistical significance ($\alpha = 0.05$) of each of the top model coefficients ($\hat{\beta}$) was then evaluated to determine its influence on the response variable (i.e., density or body length).

Top-model-predicted values of the response variables were used to visualize significant relationships with covariates. Predicted values of eel density and body length were plotted over ranges of the covariate of interest, while holding other covariates constant at mean values. Distance from the river mouth was back-transformed, if significant, to its original scale (km), before plotting by adding the mean and multiplying by the standard deviation. The mean and standard deviation of scaled values were obtained from the scale function in base R. A 95% confidence interval (CI) was plotted for predicted values of eel density.

2.4 | Female eel presence models

Logistic regression with a binomial distribution was used to evaluate how presence of eel with female gonad tissue was affected by geographic and biological variables. The binary response variable was the presence of eel with female gonad tissue. Identifiable females were indicated by a value of 1 and those without identifiable female gonad tissue (i.e., those that were classified as male, undifferentiated or undetermined) were indicated by a value of 0. Model assumptions were tested for multicollinearity among covariates using variance inflation factors and correlation coefficients (Zuur et al., 2009). Covariates included in the global model were river basin, distance from the river mouth, body length, an interaction between distance from the river mouth and body length, and an interaction between distance from the river mouth and river basin. Density of American Eel was considered, but was excluded from the global model due to collinearity. Covariates and interactions were selected based on statistically significant covariates from previously-described density and body length models and previously documented relationships (Goodwin & Angermeier, 2003; Krueger & Oliveira, 1999; Kwak et al., 2019; Smogor et al., 1995; Vélez-Espino & Koops, 2010).

Models of eel with female gonad tissue were ranked using the same procedure used for density and body length models, and pseudo-R^2 values were used to assess goodness of fit. Model averaging was conducted with the MuMIn R package using the 95% confidence set of logistic regression models to account for model selection uncertainty (Burnham & Anderson, 2002). The 95% confidence set consisted of models with a cumulative $AICc_i$ weight ≥0.95 (Burnham & Anderson, 2002).

Predicted probabilities of finding eel with female gonad tissue were plotted using model averaged coefficients and the top model to visualize significant relationships with covariates. First, the predicted log-odds values of finding eel with female gonad tissue were obtained over the range of the predictor variable, while holding all other covariates constant at their mean values for each river basin or season, if included in the confidence set of models. The predicted log odds of finding eel with female gonad tissue were converted into probabilities by exponentiating each log odd value and dividing it by 1 minus the exponentiated log odds value. Back transformation and plotting of these values followed the same procedure used for density and body length models.

3 | RESULTS

3.1 | Population characteristics

Of 287 American Eel caught in five river basins in Puerto Rico between November 2020 and August 2021 (Tables 2 and 3), 11 were sampled outside of the reach to increase sample size for sex determination, mainly during the dry season in 2020–2021. American Eel were present at 19 of 23 sampling sites (83%) during the dry season and at 13 of 14 sites (93%) during the wet season (Table 2). Most sites were depleted by sampling during the dry season (17 of 19 sites = 89%) and wet season (11 of 13 sites = 85%). Density varied among sampling locations and seasons, with a mean density of 156.7 fish/ha and a maximum density of 700.5 fish/ha during the wet season (Table 2). American Eel density was generally higher closer to the mouth of the river (Table 1; Table 2). Of 233 individuals dissected for sex determination (Table 3), 55 (19%) had visibly developed gonad tissue. Of 287 total caught, 52 (18%) were female, 3 (1%) were male, 79 (28%) were undifferentiated (body length <200 mm), and 153 (53%) were undetermined (body length ≥200 mm) (Table 3). Female eel had a mean body length of 463 mm, mean weight of 203 g, and

TABLE 2 Total catch *within stream reaches* and population density estimates of American Eel at 23 sites across five river basins in Puerto Rico during the dry (November 2020–January 2021) and wet sampling seasons (June 2021–August 2021).

		Dry season (2020–2021)		Wet season (2021)	
River basin	Sampling site	Total catch	Population density (fish/ha) ± SE	Total catch	Population density (fish/ha) ± SE
Río Piedras	46C	13	198.4 ± 1.072	1	25.29 ± 51.34
	46A	2	49.16 ± 25.51	6	80.28 ± 18.46
	46B	1	25.85 ± 0	2	49.54 ± 0
	RP2	6	257.1 ± 207.4	2	66.40 ± 12.75
Río Mameyes	4Q	0	0	27	328.1 ± 59.58
	4 K	27	669.3 ± 43.76	29	700.5 ± 98.49
	RM2	8	327.6 ± 43.23	6	187.8 ± 31.29
	4I	13	221.5 ± 56.77	10	126.6 ± 10.87
	4F	5	54.36 ± 38.50	5	44.51 ± 1.495
	4D	5	143.5 ± 4.820	3	89.46 ± 138.9
Río Sabana	[a]5C	17	–	–	–
	5A	18	319.8 ± 14.37	–	–
	RS5	18	329.7 ± 34.71	–	–
	5D	0	0	–	–
	RS4	0	0	–	–
Río Matilde	28D	6	169.6 ± 4.027	6	175.7 ± 11.01
	28E	0	0	0	0
	28C	9	323.0 ± 100.4	2	80.13 ± 0
	28B	1	24.31 ± 0	2	49.57 ± 0
Río Guanajibo	RG3	5	148.4 ± 13.16	–	–
	35H	3	92.80 ± 8.225	–	–
	35B	8	157.1 ± 2.155	–	–
	RG2	10	124.1 ± 2.947	–	–
Total catch/Mean density ± SE		175	165.3 ± 34.54	101	143.1 ± 48.41

Note: *Eleven additional eel were caught outside of sampling reaches during the dry season and were not included in density calculations*. Population density estimates were calculated using the Carle-Strub removal method, applied to 3-pass pulsed DC electrofishing data obtained from closed populations. Cells denoted with (–) indicate sites that were not sampled during the wet season.

[a]Sampling site data was not used for density models.

maximum length of 702 mm. Male eel had a mean body length of 260 mm, a mean weight of 28.7 g, and a maximum body length of 290 mm (Table 3). One American Eel with a body length of 505 mm and wet weight of 149 g was identified as undetermined due to the absence of gonad tissue in the body cavity (Table 3). Mean body lengths and weights of American Eel from southwestern rivers (Río Matilde and Río Guanajibo) were greater than those in the north and northeastern parts of the island (Table 4).

3.2 | Density and body length

Ten candidate linear regression models were fit to American Eel density and body length. Data from sampling site 5C were excluded from density models because area of the sampling reach could not be accurately estimated. Density was strongly associated with distance from the river mouth (Table S1) and eel density declined significantly ($\alpha = 0.05$) with distance from the river mouth (Table S2; Figure 2). Therefore, eel density was not included as a covariate in body length models due to the correlation with distance from the river mouth (Spearman correlation coefficient of −0.7). Body length was strongly associated with distance from the river mouth, river basin, and the interaction between these two covariates (Table S1). A second model that included distance from the river mouth, season, river basin, and an interaction between distance from the river mouth and river basin as covariates (delta-AICc$_i$ ≤2) was not considered, because it's AICc$_i$ weight was 0.42 (85%) less than the top model and inferences were similar between both models (Table S1). Eel body length was significantly related to distance from the river mouth ($\alpha = 0.05$) and increased with distance from the river mouth across Puerto Rico (Table S2; Figure 3). The positive relationship between body length and distance from the river mouth was less strong in the Río Sabana basin than other river basins, and body length did not increase with distance to river mouth in the Río Piedras basin (Figure 3). Despite

TABLE 3 Number of eel captured in each sex category and respective mean body length and weight of 287 American Eel caught at 23 sampling sites in five river basins in Puerto Rico during the dry (November 2020–January 2021) and wet seasons (June 2021–August 2021).

Sex	*N*	Mean body length (mm) ± SE	Min-max	Mean weight (g) ± SE	Min-max
Female gonad tissue	52	463 ± 13.8	244–702	203 ± 19.3	22–695
Male gonad tissue	3	260 ± 27.7	205–290	28.7 ± 7.3	14–36
Undifferentiated (<200 mm)	79	152 ± 4.5	65–197	7.35 ± 1.0	1–80
Undetermined (≥200 mm)	153	272 ± 4.0	200–505	38.0 ± 1.8	7–149
Total	287				

Note: *Eleven eel were caught outside of sampling reaches during the dry season*. We dissected 233 eel and identified the presence and absence of gonadal tissue types. All uncollected eel had body lengths <200 mm and were identified as undifferentiated. Female and male tissues were identified using macroscopic examination of gonads and the gonad squash technique was applied when macroscopic identification was not possible. American Eel with absent or incomplete gonadal tissue were identified as *undifferentiated* for eel with body length <200 mm and *undetermined* for eel with body length ≥200 mm to account for misidentification from the techniques used.

these differences between individual rivers, the overall relationship between eel body length and distance to the river mouths was positive (Table S2). Generally, predicted mean eel length was less than 400 mm from 2 to 10 km from the river mouth and greater than 400 mm above 10 km (Figure 3).

3.3 | Female eel presence

Of the 11 logistic regression models fit to data regarding the presence and absence of eel with female gonad tissue, a model with distance from the river mouth, body length, and an interaction between the two covariates had the lowest $AICc_i$ value and was considered the top model (Table S1). Two other models had delta-$AICc_i$ values ≤2 and similar $AICc_i$ weights as the top model (Table S1). The second-ranked model included distance from the river mouth, body length, river basin, and an interaction between distance from the river mouth and body length as covariates, and the third-ranked model included body length as the only variable (Table S1). Pseudo-R^2 values of the three models (range = 0.70–0.75) indicated similar predictive ability (Table S1). Body length was a significant covariate of the model-averaged 95% confidence set of models, while distance from river mouth and other covariates were not significant ($\alpha = 0.05$) (Table S2). The coefficient for scaled body length indicated a 99% probability that the likelihood of finding eel with female gonad tissue increased as body length increased (Table S2). The probability of finding eel with female gonad tissue increased sharply at ~300 mm, reached 50% at ~350 mm, and reached 99% at ~450 mm in all river basins (Figure 4). In four of five river basins, model-average predicted probabilities of eel having female gonad tissue ranged 0–11% at 2–5 km from the river mouth, 0.03–54% at 5–10 km from the river mouth, and 0.8–81% at 10 km from the river mouth (Figure 5).

Distance from river mouth, body length, and their interaction were significant predictors of female presence ($\alpha = 0.05$) in the top three logistic regression models (Table S3). These models indicate the probability of finding eel with female gonad tissue increased 75–79% as distance from river mouth increased (Table S3). The probability of finding eel with female gonad tissue increased 98–100% as body length increased (Table S3). A significant interaction between distance from the river mouth and body length was present in two of the top three models (Table S1; Table S3). The effect of distance from the river decreased 19–24% when body length increased, and the effect of body length decreased 19–24% when distance from river mouth increased (Table S3).

For the top model, the predicted probability of finding eel with female tissue included 0% at ≤200 mm and steeply increased at 300 mm (Figure S1). The predicted probability of finding eel with female gonad tissue was close to 0% at 2–10 km from the river mouth and reached ~25% at 17 km from the river mouth (Figure S1).

4 | DISCUSSION

Our first island-wide evaluation of longitudinal patterns of American Eel population characteristics in the Caribbean expands on prior studies from Puerto Rico (Kwak et al., 2019; Roghair et al., 2014). In Puerto Rico, eel density decreased with distance from the river mouth and low-density upstream environments harbored larger eel, which had a greater probability of being female. Similar patterns, observed in American Eel in temperate locations, have been posited as being explained by conspecific density-dependent size and sex determination (Goodwin & Angermeier, 2003; Krueger & Oliveira, 1999). Furthermore, because females greatly outnumbered males among those with identifiable gonad tissue, and due to proximity to the spawning location in the Sargasso Sea, Caribbean American Eel could have high reproductive potential and significantly contribute to the spawning stock of this widely dispersed population. Expanded knowledge of the species' ecology throughout its entire range is imperative, as well as implementing management efforts to ensure stream connectivity to optimal upstream eel habitat.

TABLE 4 Mean body lengths and weights of 287 American Eel caught at each sampling site (11 eel were caught outside of sampling reaches during the dry season) at 23 locations across five rivers in Puerto Rico during the dry (November 2020–January 2021) and wet sampling seasons (June 2021–August 2021) seasons.

		Dry season (2020–2021) (*N* = 185)				Wet season (2021) (*N* = 102)			
River	Sampling site	Mean length (mm) ± SE	Min–max	Mean weight (g) ± SE	Min–max	Mean length (mm) ± SE	Min–max	Mean weight (g) ± SE	Min–max
Río Piedras	46C	337 ± 24.5	225–495	84.5 ± 20.7	14–236	214 ± 0	214–214	15.0 ± 0	15–15
	46A	375 ± 81.2	275–536	133 ± 86.3	34–305	302 ± 22.9	219–373	63.3 ± 14.2	23–105
	46B	305 ± 0	305–305	46 ± 0	46–46	372 ± 29.5	340–431	89.3 ± 26.9	60–143
	RP2	301 ± 41.6	179–471	67.1 ± 29.2	7–227	398 ± 97.0	301–495	145 ± 99	46–244
Río Mameyes	4Q	NP	NP	NP	NP	174 ± 20.1	65–330	20.1 ± 4.6	1–79
	4K	246 ± 8.7	163–312	29.8 ± 3.4	3–60	266 ± 19.1	135–702	58.3 ± 23.0	5–695
	RM2	278 ± 46.6	182–593	74.6 ± 52.0	8–438	228 ± 25.0	180–338	25.2 ± 10.6	10–76
	4I	243 ± 12.7	160–296	25.7 ± 4.3	5–47	218 ± 18.5	110–294	20.0 ± 4.2	2–41
	4F	264 ± 50.1	148–439	48.0 ± 21.0	3–132	225 ± 26.7	154–303	23.0 ± 8.1	5–50
	4D	229 ± 22.1	175–291	19.4 ± 5.9	8–36	274 ± 47.4	180–332	31.7 ± 12.3	8–49
Río Sabana	5C	251 ± 20.2	145–460	33.8 ± 9.4	5–137	—	—	—	—
	5A	223 ± 23.0	90–645	33.3 ± 17.5	1–412	—	—	—	—
	RS5	267 ± 26.6	125–516	41.9 ± 14.0	2–229	—	—	—	—
	5D	NP	NP	NP	NP	—	—	—	—
	RS4	NP	NP	NP	NP	—	—	—	—
Río Matilde	28D	312 ± 51.2	152–448	73.3 ± 28.2	6–184	316 ± 60.9	156–570	115 ± 62.0	19–418
	28E	NP	NP	NP	NP	NP	NP	NP	NP
	28C	288 ± 64.5	155–643	113 ± 67.2	7–485	314 ± 87.5	226–401	64 ± 46.0	18–110
	28B	577 ± 0	577–577	329 ± 0	329–329	526 ± 24.5	501–550	267 ± 29.5	237–296
Río Guanajibo	RG3	204 ± 38.6	153–358	20.2 ± 13.2	5–73	—	—	—	—
	35H	471 ± 7.2	462–485	197 ± 15.0	174–225	—	—	—	—
	35B	442 ± 19.7	375–516	141 ± 15.8	91–226	—	—	—	—
	RG2	468 ± 30.1	363–644	197 ± 43.4	84–475	—	—	—	—

Note: Cells denoted with (—) indicate sites that were not resampled during the wet season and cells denoted with "NP" indicate sites where eel were not present.

We generalized previously observed patterns in American Eel density and body length in relation to distance from the river mouth at the southern edge of this species' range. Our sampling had extensive spatial coverage of Puerto Rico's American Eel habitat in river basins where most upstream habitats were still accessible to eel (Cooney & Kwak, 2013). We found that eel density decreased with increasing distance from river mouths in Puerto Rico. This result agrees with studies of eel in temperate regions, where density was negatively related to upstream distance, especially in rivers with instream barriers (Smogor et al., 1995; Wiley et al., 2004). In Puerto Rico, American Eel body length increased with distance from the river mouth, which was consistent with temperate regions where larger eel were further inland or upstream of in-stream barriers and smaller individuals were common in downstream and brackish water environments, especially in dammed rivers (Goodwin & Angermeier, 2003; Helfman et al., 1984; Machut et al., 2007; Smogor et al., 1995).

Our findings also generalized the idea that upstream freshwater habitats were more likely to harbor longer eel that were more likely to be female than downstream habitats. In Puerto Rico, longer American Eel have a higher probability of being female with a sharp increase in eel with female gonad tissue at ~300 mm body length. Furthermore, longer American Eel are more frequently in farther upstream environments. In Puerto Rico, longer eel are expected to occur at distances greater than 10 km from the river mouth. Though distance from the river mouth was not a significant covariate of female gonad tissue presence in our averaged model. The overall biological significance of distance from the river mouth was evident from the separate top models for female gonad tissue presence and the significant relationship between body length and distance from the river mouth. Taken together, these models indicated that female eel were more likely to occur at distances farther upstream, rather than close to a river mouth. We found that the probability of eel with female gonad tissue were low and eel were shorter in length up to 11 km from river mouths, while longer eel were found in the largest river basins with sampling sites located more than 11 km upstream (except in the Río Guanajibo). In the Río Guanajibo, eel with

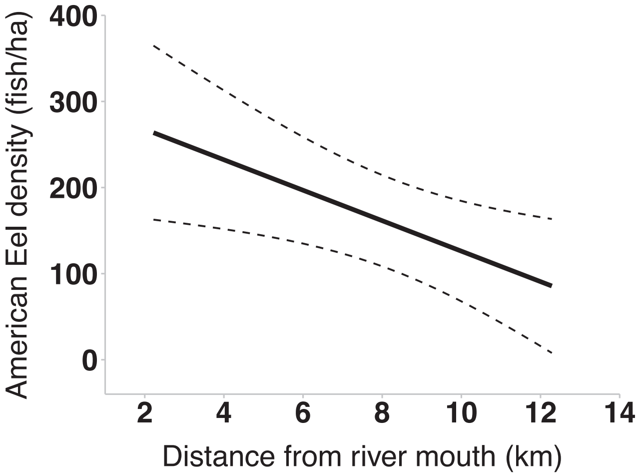

FIGURE 2 Predicted American Eel density vs. distance from river mouth obtained from the linear regression model with the independent variable distance from the river mouth ('dtm'). This top model was developed by fitting a linear regression model to 36 data points of scaled distance from the river mouth and eel density sampled during the dry season (November 2020–January 2021) and wet season (June 2021–August 2021) in Puerto Rico. Predicted values are given by the solid line and the 95% confidence intervals are given by the dashed lines. Scaled distance to mouth values displayed on the x-axis were back transformed to their original scale in kilometers.

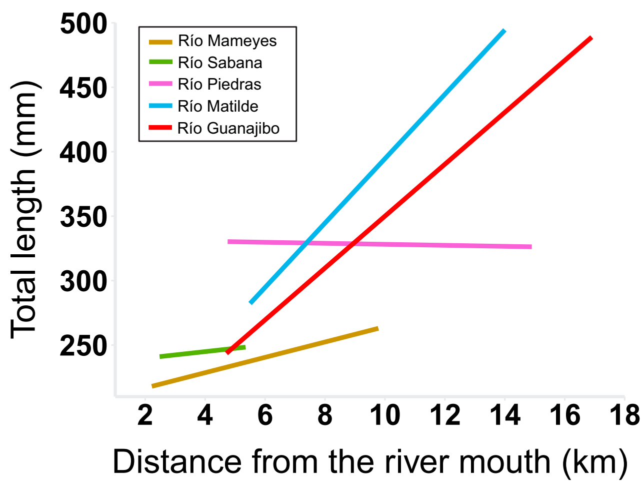

FIGURE 3 Predicted American Eel body length vs. distance from the river mouth for each of the five river basins sampled in Puerto Rico during the dry season (November 2020–January 2021) and wet season (June 2021–August 2021). These values were calculated by fitting the linear regression model containing distance from the river mouth ('dtm'), river basin, and an interaction between the two covariates to 287 observations of American Eel body length and scaled distance from river mouth ('dtm'). Scaled distance from the river mouth values displayed on the x-axis were back transformed to their original scale in kilometers.

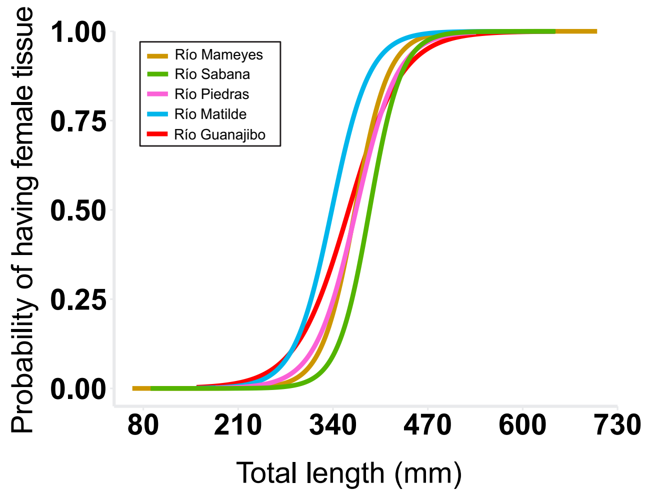

FIGURE 4 Probability of finding American Eel with female gonad tissue given eel body length across five river basins sampled in Puerto Rico during the dry season (November 2020–January 2021) and wet season (June 2021–August 2021). These predicted values were calculated by using the full model averaged coefficients from the 95% confidence set of logistics regression models containing the covariates: distance from the river mouth ('dtm'), body length, an interaction between distance from the river mouth ('dtm') and body length, river basin, and an interaction between distance from the river mouth ('dtm') and American Eel body length river basin. Scaled body length values displayed on the x-axis were back-transformed to their original scale in millimeters.

female gonad tissue were predominant at all the sampling locations, perhaps due to downstream migration of silvering eel (Haro, 2003; Jessop, 1987). Overall, our results, coupled with those from North America and Canada (e.g., Bonvechio et al., 2018; Côté et al., 2015; Helfman et al., 1984; Oliveira, 1999) showed that low density upstream environments are crucial for production of female American Eel across the species' range.

We were unable to identify high density downstream sites as male dominated habitats due to the low number of eel with male gonad tissue in our samples (Helfman et al., 1987; Oliveira, 1999; Thibault et al., 2007). Limitations of our study included sex determination wherein immature yellow eel ≥200 mm TL may have been misidentified as not containing differentiated tissue using the gonad squash technique (Krueger & Oliveira, 1997). Our samples were 81% undetermined or undifferentiated eel. Sex ratio was heavily skewed towards females (52:3), similar to another study (Kwak et al., 2019). This highly disproportionate sex ratio was comparable to results from North America and Canada, where eel with male gonad tissue were rare (Gray & Andrews, 1970; Hansen & Eversole, 1984). In temperate regions, males dominated sex ratios in high-density river systems (Krueger & Oliveira, 1999). Our results differed from rivers where high proportions of undifferentiated individuals characterized male-dominated sex ratios and suppression of females (Krueger & Oliveira, 1999).

Collectively, our findings indicated that Caribbean American Eel may exhibit the same longitudinal patterns in density, body length, and sex as in temperate North American regions. Across the species' range, distance from river mouths may play a significant role in the size and sex of American Eel, which may also be affected by conspecific density (Davey & Jellyman, 2005; Krueger & Oliveira, 1999; Oliveira & McCleave, 2000). Low-density upstream environments

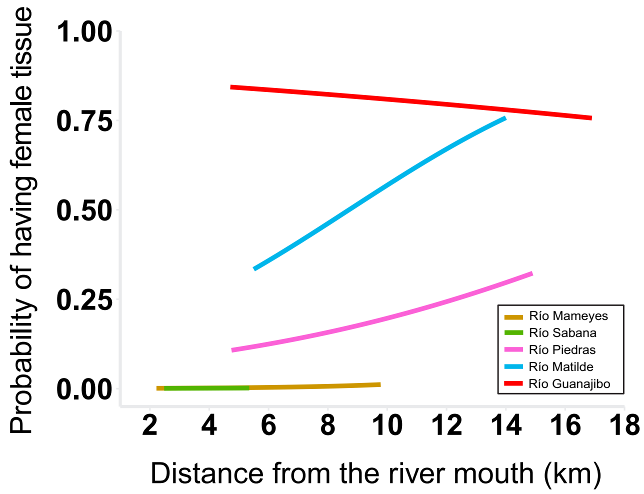

FIGURE 5 Probability of finding eel with female gonad tissue given the distance from the river mouth across five river basins sampled in Puerto Rico during the dry season (November 2020–January 2021) and wet season (June 2021–August 2021). These predicted values were calculated by using the full model averaged coefficients from the 95% confidence set of logistics regression models containing the covariates: distance from the river mouth ('dtm'), body length, an interaction between distance from the river mouth ('dtm') and body length, river basin, and an interaction between distance from the river mouth ('dtm') and river basin. Scaled distance from the river mouth ('dtm') values displayed on the x-axis were back-transformed to their original scale in kilometers.

harbor predominantly large female eel, while high-density downstream environments may harbor smaller and primarily undifferentiated or male American Eel.

American Eel from the southern portion of the geographic range could significantly contribute to reproduction and survival of the global population of this species. Identifiable eel in Puerto Rico were dominated by females, but female eel body length is shorter in Puerto Rico than in Canada (Jessop, 2010; Kwak et al., 2019). These results agree with greater latitudes harboring larger female eel, but may differ with observations of northern latitudes contributing a significant proportion of the reproductive potential to the population (Barbin & McCleave, 1997). Though larger eel have greater fecundity, Puerto Rico and other Caribbean islands could contribute to reproductive success of the population because female eel are abundant and migrate shorter distances to reach the spawning location in the Sargasso Sea. American Eel are at high risk of predation during their long spawning migrations (Béguer-Pon et al., 2012), so shorter distance migrations from optimal habitats in Puerto Rico could reduce the risk of predation and increase the probability of successful spawning.

Our findings provide new insights into how urbanization can affect longitudinal patterns in American Eel population structure. In the Río Piedras, eel had a noticeably truncated pattern in body length distribution than all other rivers in our study. The Río Piedras is a highly urbanized river basin in the metropolitan area of Puerto Rico that is characterized by a watershed with intense urban land use, high levels of pollution, and channelization that degrades habitat (Ramírez et al., 2009). These characteristics can alter densities and population size structures of American Eel (Cooney & Kwak, 2013; Haro et al., 2000).

Our study provided critical information on effects of in-stream barriers on American Eel population structure. In-stream barriers alter American Eel density and length in river basins. Natural in-stream barriers could affect eel distribution predominantly in the Río Sabana, where American Eel were absent from upstream sites. The Río Sabana has large natural barriers in downstream sections (Roghair et al., 2014). Natural and artificial barriers can decrease eel density in upstream environments (Goodwin & Angermeier, 2003; Machut et al., 2007) while dams can extirpate eel from suitable upstream habitats (Camhi et al., 2021; Cooney & Kwak, 2013).

4.1 | Conservation and management implications

Understanding and identifying overall patterns in American Eel ecology, demographics, and threats is an ongoing challenge (MacGregor et al., 2008). American Eel are widely distributed throughout the Atlantic coast, but little is known about the status and trends of eel in the southern regions (Benchetrit & McCleave, 2016; Shepard, 2015). Our study expanded knowledge of American Eel population characteristics and patterns to the Caribbean region. Further range-wide research is needed to fully understand how habitat differences between downstream and upstream environments affect size and sex of American Eel. Our results may inform management of the global American Eel population by filling significant data gaps and providing information on anthropogenic threats to the population. Previous species assessments have relied heavily on information from northern portions of the species' range where American Eel have declined (ASMFC, 2017; COSEWIC, 2012; Jacoby et al., 2017; Shepard, 2015). However, evaluating this species across its entire distribution is necessary because it is a single, panmictic population (Cairns et al., 2022). Our findings provide new information on the potential reproductive contribution and status of American Eel from the Caribbean region, which could be used for future range-wide models and analytic assessments (ASMFC, 2017; Cairns et al., 2022). Possible truncated patterns in American Eel in urban river basins and the importance of upstream habitats revealed by our study could inform international cooperation among environmental, dam, and fisheries managers, to highlight the importance of instream passage for this species (ASMFC, 2017; Cairns et al., 2022; MacGregor et al., 2008). Prioritizing stream connectivity and habitat conservation in the Caribbean could contribute to the persistence of the entire American Eel population by ensuring the production of abundant female eel in close proximity to the global spawning location.

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CONFLICT OF INTEREST STATEMENT

All authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The research sampling was conducted under the North Carolina State University Institutional Animal Care and Use Committee IACUC #20-216 and DRNA permit #2020-IC-041 provided by Gobierno de Puerto Rico Departamento de Recursos Naturales y Ambientales. Access and animal use permit within the US Forest Service boundaries in El Yunque National Forest was granted via authorization ID YNF3010.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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