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Ecology and conservation of the American eel in the Caribbean region

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Abstract

The majority of American eel, *Anguilla rostrata* LeSueur, knowledge is derived from temperate regions in the United States and Canada, with little known from its tropical Caribbean distribution. Findings of original research on American eel distribution, abundance, population biology, habitat ecology and threats from the Caribbean island of Puerto Rico were synthesised. American eel were captured from 48 of 116 sites (41.4%) in 26 of 49 river basins (53.1%) during 2005–2016, and it was extirpated upstream of dams and migration barriers >3.0 m high (38.9% of habitat). Mean density and biomass were 438.9 fish/ha and 23.44 kg/ha, respectively. Upstream habitats favoured larger individuals, and females were larger than males. The swim-bladder parasite *Anguillicoloides crassus* Kuwahara, Niimi & Hagaki was not found in 120 eels examined. Realised threats include dams and other migratory barriers, habitat loss and alteration and pollution; exotic species and commercial fishing are impending threats; and the least understood is climate change.

KEYWORDS

Anguilla rostrata, *Anguillicoloides crassus*, dams, fish distribution, Puerto Rico, river

1 | INTRODUCTION

The American eel, *Anguilla rostrata* LeSueur, is a widely distributed, economically valuable, culturally significant and ecologically important, but imperiled fish species. It is a facultatively catadromous species (McCleave & Edeline, 2009) with multiple life stages that occur in freshwater and estuarine habitats from southern Greenland (historically) through eastern Canada and the United States to Venezuela, including Central America, northern parts of South America, the Gulf of Mexico and Caribbean regions (Figure 1: Benchetrit & McCleave, 2016; Tesch, 2003). Current knowledge confirms a single panmictic American eel population that spawns in the Sargasso Sea of the Atlantic Ocean. Phenotypic plasticity allows the species to occupy a diversity of habitats from estuaries to headwater streams and may result in multiple habitat-specific phenotypes within a region (Figure 1; Shepard, 2015). The species' international distribution and dynamic life history, biology and ecology are challenges for its scientific study and effective conservation and management, and many uncertainties and knowledge gaps remain (MacGregor et al., 2008; Vélez-Espino & Koops, 2010).

The American eel remains extant throughout much of its historical distribution, but its abundance has been drastically reduced over time. The species is in decline and at or near historically low levels throughout its US range, and the population is considered depleted (ASMFC, 2012, 2017; MacGregor et al., 2008). It is classified as Endangered by the IUCN, Threatened by the Canadian Government (but not protected under the Canadian Species at Risk Act), and it is not listed or protected under the Endangered Species Act in the United States (COSEWIC, 2012; IUCN, 2017; Shepard, 2015). The species is not protected under any global treaty or convention (e.g. CITES).

Commercial fisheries for American eel were historically prominent, are currently permitted on a limited scale, and are a presumed cause of the species decline. American eel commercial harvest currently occurs at all life stages in estuarine and inland habitats primarily in the United States and Canada under varying regulations (MacGregor et al., 2008; Shepard, 2015). The ASMFC (Atlantic States Marine Fisheries Commission) (2012) warned that current levels of fishing at all life stages may be too high for sustainability, given additional anthropogenic stressors, and additional regulations were subsequently implemented with the goal to reduce American eel mortality at all life stages (ASMFC (Atlantic States Marine Fisheries Commission), 2017). Limited commercial fishing exists on Caribbean islands and presumably in Mexico at multiple life stages. Historical and current American eel commercial landings are driven by domestic and Asian markets, rather than by stock assessment, management practices or regulations (Pawson et al., 2005; Shepard, 2015). Current commercial fisheries for the species are largely influenced by international demand, which has increased dramatically with the decline in availability of the European eel, *Anguilla anguilla* L., and Japanese eel, *Anguilla japonica* Temminck and Schlegel, in global markets. The sharply inflated and volatile market price for eels in Asia, especially glass eels for Asian aquaculture production, has presumably stimulated illegal fishing and trade and has maintained a stable, low harvest in American eel permitted commercial fisheries, even with concurrent decreasing stock trends (ASMFC (Atlantic States Marine Fisheries Commission), 2012, 2017).

In addition to commercial harvest, other interacting biological and ecological stressors threaten the American eel and contribute to its decline. Climate change, habitat loss (estuarine, lentic and lotic), barriers to migration (and hydropower operations), parasites and pathogens, and chemical contaminants may act as synergistic and additive stressors on the species (Shepard, 2015). The complex and interactive nature of these stressors, which act at multiple spatial and temporal scales within the framework of a complex life history, render identification and quantification of relative or absolute effects on the American eel population a nearly impossible challenge (Miller et al., 2009). Nonetheless, field investigations and correlational evidence along with various anecdotes and experiments associated with multiple anguillid eel species are sufficient to implicate these stressors as conservation concerns (Dekker & Casselman, 2014; Dekker et al., 2003; Miller et al., 2009).

The vast majority of research and knowledge on the American eel is derived from temperate regions in the United States and Canada, and very little is known about the species in its tropical distribution in the Caribbean and Gulf of Mexico regions (Benchetrit & McCleave, 2016; Shepard, 2015). Ocean currents disperse American eel larvae (leptocephali) from the western Sargasso Sea spawning grounds, and a majority of the population are found along the Atlantic coasts of the United States and Canada (Figure 1; Miller et al., 2009; Shepard, 2015). A lesser number may be transported via the Caribbean Current to the Gulf Loop Current, and settle in Caribbean island and mainland rivers and continental waters of the Gulf of Mexico (Kleckner & McCleave, 1982, 1985; Miller et al., 2009). Once these young eels settle in Caribbean estuarine and fresh waters, their biology and ecology are largely unknown, with their distribution in the region only recently discerned (Benchetrit & McCleave, 2016). The American eel benchmark stock assessment does not include population segments in the Caribbean, but assumes that trends in the region are similar to those modelled (ASMFC (Atlantic States Marine Fisheries Commission), 2012). However, key differences between the Caribbean and Atlantic segments of the population certainly

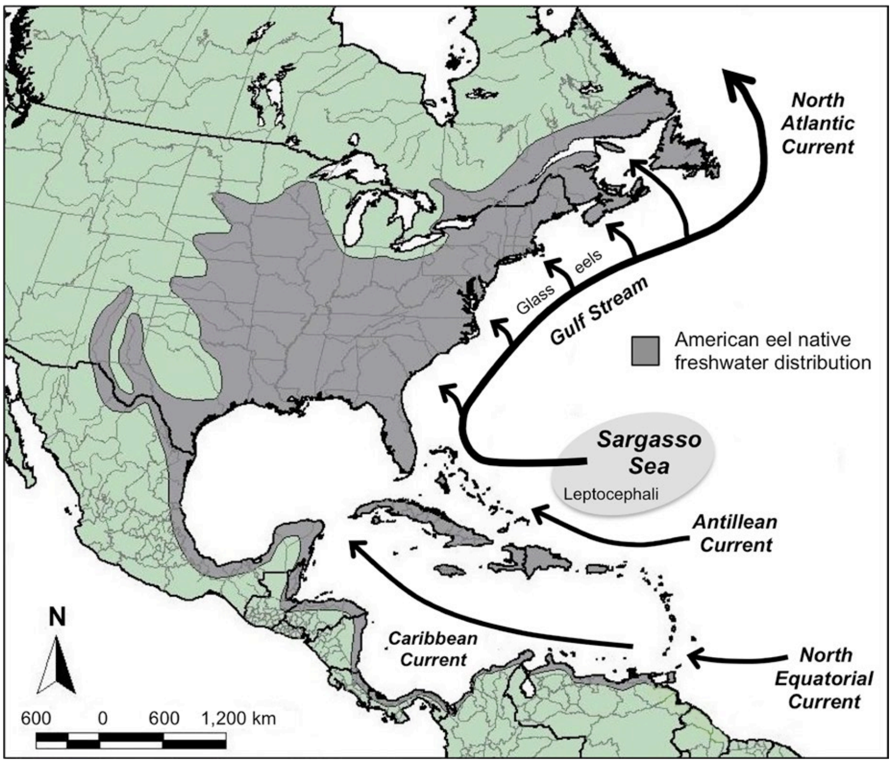


FIGURE 1 Map of the native American eel freshwater distribution, including the Sargasso Sea spawning area and ocean currents that transport larval American eels (leptocephali) to freshwater habitats (modified from Shepard, 2015) [Colour figure can be viewed at wileyonlinelibrary.com]

exist (e.g. food-web interactions; Engman, Fischer, Kwak & Walter, 2017), but data are so scant in the Caribbean that the assumption remains equivocal and highlights the urgent need for information on the American eel in this region to guide conservation and management of the species.

In response to the information gap and data needs for the American eel in the Caribbean region, findings of original research by the authors and their associates on American eel distribution, abundance, population biology, habitat ecology, and stressors and threats from the Caribbean island of Puerto Rico were synthesised and presented. Puerto Rico is an ideal island setting to study human influences on freshwater and diadromous fishes because of an extremely dense human population and the associated demands for water and activities that impact freshwater and marine ecosystems and fisheries (Kwak, Engman, Fischer & Lilyestrom, 2016; Ramírez, Engman, Rosas, Perez-Reyes & Martinó-Cardona, 2012). Various ecological processes and components of the stream and river fish assemblages of Puerto Rico have been studied for over a decade, with the goal of providing critical information to guide the conservation and management of the lotic resource (Kwak, Cooney & Brown, 2007; Kwak, Smith, Buttermore, Cooney & Cope, 2013; Kwak et al., 2016; Neal, Lilyestrom & Kwak, 2009). This research effort has yielded insight and knowledge that is specific to the American eel, which may serve to identify and elucidate spatial and temporal trends, ecological functions, and population drivers to inform natural resource agencies in strategic conservation and management planning and implementation of such plans.

2 | METHODS

Fish assemblages were quantitatively sampled in 116 stream and river reaches of 49 major drainages island-wide in Puerto Rico from 2005 to 2016, including two sites on the island of Vieques (Figure 2; Kwak et al., 2007, 2013). Stream reaches 65–150 m in length were sampled using pulsed-DC electrofishing techniques (single or multiple backpack electrofishers or a barge electrofisher) following a standardised three-pass removal procedure to estimate population density and biomass for each species at each site. Each fish was measured for total length (mm) and weighed (g). During 2015–2016, 120 American eels from four river drainages were sacrificed, accurately measured for length and weight, examined for the presence of gonads to determine sex, and swim bladders were excised and examined for the presence of the exotic, parasitic nematode *Anguillicoloides crassus* Kuwahara, Niimi & Hagaki. *Anguillicoloides crassus* is highly invasive and can cause severe impairment of anguillid eel swim bladders, reduced swimming ability, related health effects and mortality in some cases (Kirk, 2003).

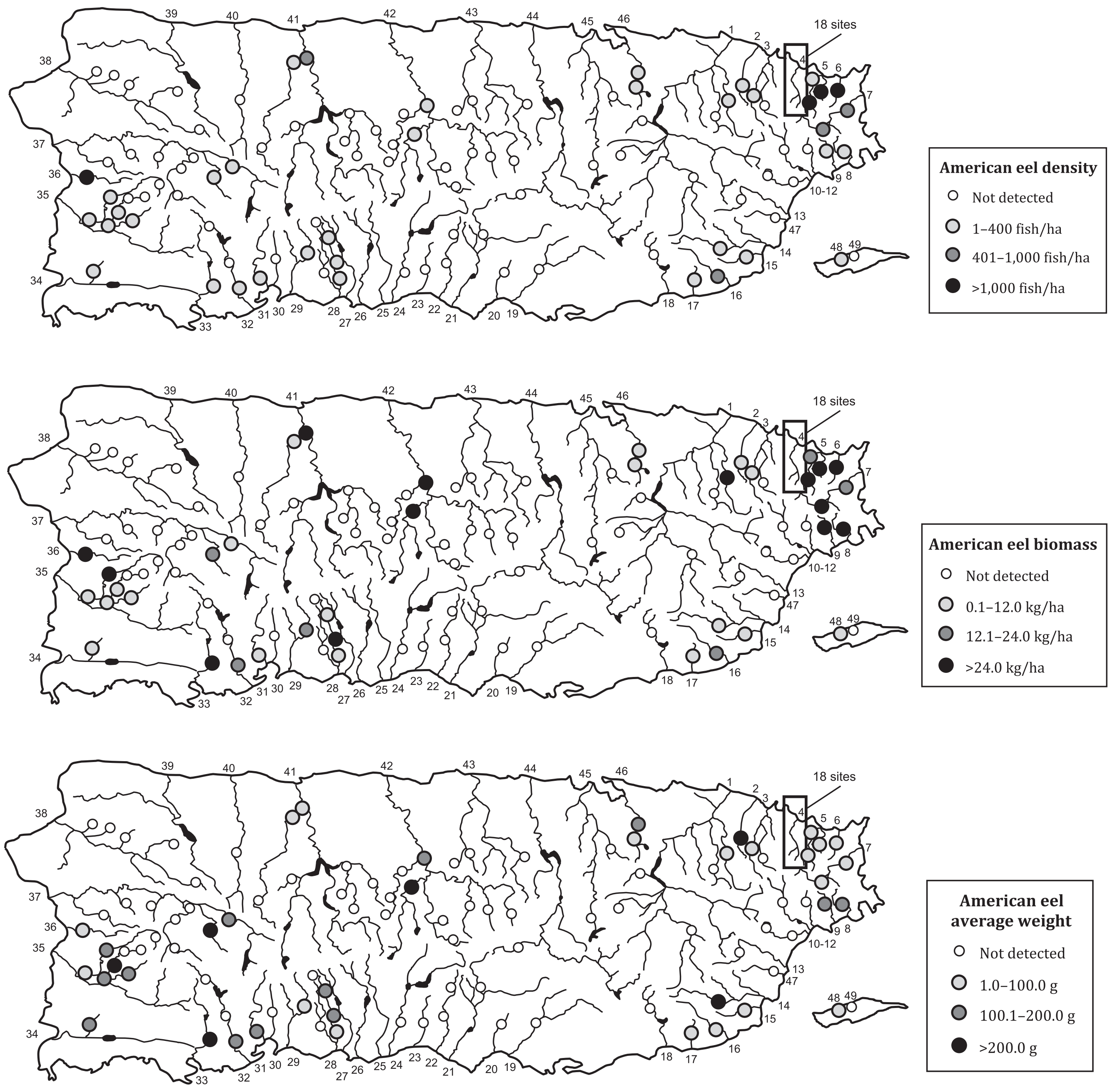
Habitat surveys were conducted at each site and included measurements of instream physical habitat, water quality parameters and riparian features. Catchments upstream of the sampling sites were delineated, and land cover and ownership of respective catchments and riparian zones were derived from existing geospatial data provided by the Puerto Rico Gap Analysis Project (https://data.fs.usda.gov/geodata/other_fs/IITF/index.php). A total of 335 dams and other instream barriers in Puerto Rico were identified and physical characteristics of each barrier surveyed. Details of the fish sampling gears, procedures, population parameter estimation and habitat surveys were presented by Kwak et al. (2007), and instream barrier survey techniques described by Cooney and Kwak (2013). When synthesised and integrated, these extensive surveys of fish assemblages and multi-scale environmental characteristics provide substantial knowledge and insight into American eel distribution and abundance, population biology, habitat relations, and associated stressors.

3 | RESULTS AND DISCUSSION

3.1 | Distribution and abundance

American eel were collected and population size estimated at 48 of 116 sites sampled (41.4%) in 26 of 49 river basins (53.1%) in Puerto Rico during 2005–2016 (Figure 2). The occurrence of American eel was greatly influenced by instream barriers to upstream migration, and the species was not detected at any site surveyed upstream of a reservoir impounded by a high dam or upstream of low-head dams or barriers exceeding 2.5 m in height. The species was present at most downstream sites and those without instream migration barriers downstream of the sampling site. It was detected at 1 of 2 sites on the island of Vieques and 9 of 18 sites sampled on the Mameyes River, one of very few free-flowing, unimpounded rivers of the island (Figures 2 and 3). Fish surveys by Roghair, Krause, Cano and Dolloff (2014) targeting American eel in El Yunque National Forest streams, including the Mameyes River, found similar occurrences and densities of the species. The patchy within-river distribution of the species is demonstrated by the discontinuous longitudinal pattern in the species detections in the Mameyes River (Figure 3).

American eel abundance estimates varied widely, averaged 438.9 fish/ha, and ranged to over 3,000 fish/ha in density, with a mean biomass of 23.44 kg/ha up to over 180 kg/ha (Table 1). The highest densities were estimated for downstream sites, and especially those in the northeastern portion of the island where catchments are within protected areas of the El Yunque National Forest and other public lands. Most of the downstream sites with high densities of American eel also yielded high biomass estimates, with some exceptions (Figure 2). Several high-elevation inland sites with low or moderate densities of the species, showed relatively high mean weight and moderate biomass. Examples of high mean individual weight of American eels, occurring at inland, upstream sites are especially evident in the Añasco, Guanajibo, Matilde and Manatí drainages (Figure 2). Island-wide extensive sampling and intensive sampling in the Mameyes River revealed patchy occurrence and a general trend of large eels found in low to moderate densities in high-elevation inland sites, relative to high densities of smaller individuals at sites more proximate to the river mouth and coast.



1. Loíza
2. Herrera
3. Espíritu Santo
4. Mameyes
5. Sabana
6. Juan Martín
7. Fajardo
8. Dagüao
9. Palma
10. Santiago
11. Blanco
12. Antón Ruiz
13. Humacao
14. Guayanés
15. Caño de Santiago
16. Maunabo
17. Jaraboa
18. Patillas
19. Salinas
20. Jueyes
21. Coama
22. Descalabrado
23. Cañas
24. Jacaguas
25. Inabón
26. Bucaná
27. Portugés
28. Matilde
29. Tallaboa
30. Macaná
31. Guayanilla
32. Yauco
33. Loco
34. Cartagena
35. Guanajibo
36. Yagüez
37. Añasco
38. Culebrinas
39. Guajataca
40. Camuy
41. Arecibo
42. Manatí
43. Cibuco
44. La Plata
45. Bayamón
46. Piedras
47. Candelero
48. Cofresí
49. Unnamed

FIGURE 2 Occurrence and density (top), biomass (middle), and average weight (bottom) of American eel among 116 stream and river sites sampled during 2005 to 2016 spanning 49 drainage basins in Puerto Rico (see Figure 3 for 18 sites in the Mameyes River [basin number 4]). Density and biomass were estimated using a three-pass removal procedure following a standardised protocol described by Kwak et al. (2007)

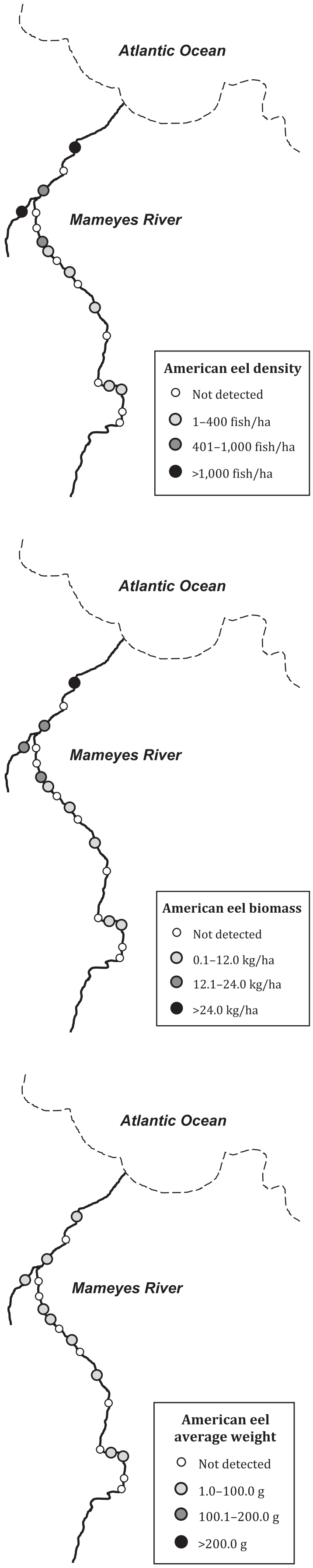


FIGURE 3 Occurrence and density (top), biomass (middle), and average weight (bottom) of American eel among 18 sites in the Mameyes River, Puerto Rico, sampled during 2005 to 2016. Density and biomass were estimated using a three-pass removal procedure following a standardised protocol described by Kwak et al. (2007)

TABLE 1 American eel population characteristics (mean, standard deviation [*SD*], and minimum–maximum) from 48 stream and river sites in Puerto Rico where the species was sampled 2005–2016

Variable	Mean	*SD*	Min–Max
Fish density (fish/ha)	438.60	730.78	11.60–3,124.50
Fish biomass (kg/ha)	23.44	36.52	0.50–182.90
Mean individual fish weight (g)	117.86	118.13	3.87–470.30

Note. Density and biomass were estimated using a three-pass removal procedure following a standardised protocol described by Kwak et al. (2007). Mean individual weight statistics represent the among-site average of the mean weight at each site.

TABLE 2 Length and weight statistics (mean, standard deviation [*SD*], and minimum–maximum) for 43 American eels of known sex collected from four Puerto Rico rivers 2015–2016

Statistic	Male (*N* = 9)	Female (*N* = 34)
Total length (mm)		
Mean	335.3	442.6
SD	92.4	127.3
Min–max	246–563	248–735
Weight (g)		
Mean	80.4	204.9
SD	92.2	215.4
Min–max	23–324	25–982

3.2 | Population biology

The 120 American eels accurately measured and examined for sex and the swim-bladder parasite revealed new and relevant information on the species population biology in Puerto Rico. Of those fish with sufficiently developed gonads, nine were male and 34 were female (male:female sex ratio of 1:3.78). American eels identified as female were substantially larger by length and weight than those identified as male (Table 2; Figure 4). On average, females were 107.3 mm longer and 124.5 g heavier than males. Both sexes of American eels and smaller fish of undetermined sex appeared to follow a common length–weight relationship (Figure 4, $\log_{10}$Weight = −6.2668 + 3.1958; $\log_{10}$Total length; r^2 = 0.988; p = 0.0001). These differences in size imply that the distributional trend of occurrences of heavier individuals at lower densities at

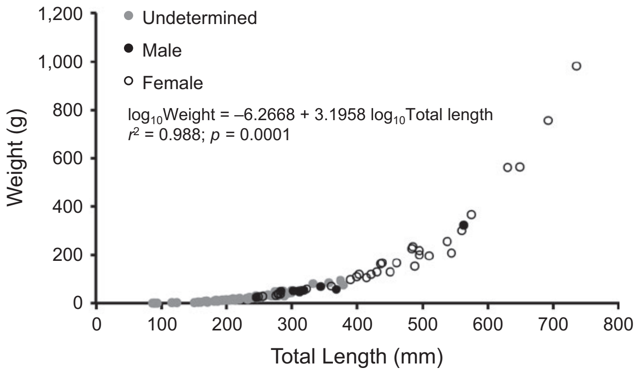


FIGURE 4 Length–weight biplot of 120 American eels collected from four Puerto Rico rivers (Arecibo, N = 25; Cofresí, N = 1; Mameyes, N = 92; Piedras, N = 2) according to known (N = 9 males, 34 females) or undetermined (N = 77) sex

upstream sites indicate that upstream habitats contain relatively high proportions of females. The slope of the length-weight relationship of American eels in Puerto Rico (3.196) was slightly lower than an overall mean (3.25) and within a general range (3.06–3.29) of regional mean slopes for US Atlantic Coast American eels, with the exception of a lower slope (2.52) for American eel in southern New England (ASMFC (Atlantic States Marine Fisheries Commission), 2017).

Sex determination in the American eel is known to be environmentally influenced (McCleave, 2001; Tesch, 2003). Factors such as habitat type, latitude, salinity, productivity, eel density and growth can determine sex (Côté, Castonguay, Verreault & Bernatchez, 2009; Fenske, Secor & Wilberg, 2010; Oliveira & McCleave, 2000; Vélez-Espino & Koops, 2010). Specifically, previous studies from the temperate region of this species distribution showed that habitats with high conspecific densities lead to male-dominated sex-ratios, while females tend to occur in low-density habitats (Krueger & Oliveira, 1999). Therefore, the lower densities of eels, as observed in some upstream, high-elevation reaches in Puerto Rico, were likely to have female-dominated sex ratios, while the downstream, high-density environments may favour male differentiation (Tesch, 2003). This finding has relevant conservation implications for Caribbean rivers, wherein upstream, high-elevation reaches that may favour females are made unavailable to American eels by high dams, resulting impounded reservoirs and other migration barriers.

Of the 120 American eels examined for the presence of the parasitic swim-bladder nematode *Anguillicoloides crassus*, none were parasitised by the worm. *Anguillicoloides crassus* infections in the American eel are widespread in United States and Canadian waters (Shepard, 2015), but no occurrence records are known from the Caribbean. The apparent lack of infection in American eels in Puerto Rico may be related to water temperature, salinity of estuaries, or because *Anguillicoloides crassus* has not yet been introduced via anthropogenic means.

3.3 | Habitat relations

The widespread distribution of the American eel within and among Puerto Rico rivers reflects broad tolerance to environmental conditions. The species was found in river reaches with widely varying habitat conditions, ranging from small, high-elevation, high-gradient streams to large, low-gradient streams in the coastal plain. The means of measured physical parameters of reaches occupied by American eels represent the average of widely varying conditions and indicate conditions of moderate stream width, shallow depth, low velocity, predominantly coarse substrate materials, a moderate bank angle and abundant physical instream cover (Table 3). Water quality measurements at occupied reaches represent typical stream water conditions found on the island, ranging from low-fertility, cool, small streams to larger more fertile, nutrient-enriched and human-impacted rivers (Table 4). The riparian and watershed land cover of occupied reaches similarly reflect the diversity of the landscape over the island, ranging from primarily forested landscapes to highly urbanised settings (Table 5). The tolerance and plasticity of the species are further demonstrated by the American eel's common occurrence in the most urbanised stream habitats on the island. For example, American eels were found at relatively low densities (47.3–103.9 fish/ha; N = 4; Figure 2) at both sites sampled in the Río Piedras, a river that flows through the San Juan metropolitan area. Riparian land cover at these sites ranged from 33.0% to 34.3% and 34.4% to 39.4% urban at the watershed scale, representing the most human-dominated river basin on the island.

TABLE 3 Sampling reach characteristics (mean, standard deviation [*SD*], and minimum–maximum) measured at 48 stream and river sites in Puerto Rico where American eels were collected 2005–2016

Variable	Mean	*SD*	Min–Max
Reach length (m)	133.79	22.45	65.00–150.00
Width (m)	8.41	4.35	2.61–20.31
Area (m^2)	1082.67	481.28	212–2,033
Depth (cm)	18.88	7.98	8.2–39.6
Velocity (m/s)	0.19	0.15	0.02–0.62
Dominant substrate (mode)	Small cobble (64-130 mm diameter)	–	–
Bank angle (°)	135.04	15.81	100.50–167.30
Cover (%)	57.62	19.04	16.00–98.00

TABLE 4 Water quality characteristics (mean, standard deviation [*SD*], and minimum–maximum) measured at 48 stream and river sites in Puerto Rico where American eels were collected 2005–2016

Variable	Mean	*SD*	Min–Max
Temperature (°C)	25.36	2.15	21.68–29.97
Dissolved oxygen concentration (mg/L)	7.90	1.29	4.1–10.98
pH	7.88	0.52	6.40–9.18
Conductivity (μS/cm)	294.06	123.00	121.00–668.00
Salinity (ppt)	0.15	0.08	0.06–0.55
Alkalinity (mg/L $CaCO_3$)	111.93	52.55	33.00–248.00
Hardness (mg/L $CaCO_3$)	115.89	56.35	38.00–248.00
Total dissolved solids (g/L)	0.19	0.08	0.08–0.43
Turbidity (FAU)	4.16	3.68	0–14.00
Nitrate concentration (mg/L NO_3^-)	2.59	3.15	0–14.40
Nitrite concentration (mg/L NO_2^-)	0.04	0.08	0–0.456
Ammonia concentration (mg/L NH_3)	0.06	0.13	0–0.50
Phosphorus concentration (mg/L PO_4)	0.49	0.53	0–2.75

TABLE 5 One hundred metre riparian buffer and watershed characteristics (land cover and ownership mean, standard deviation [*SD*], and minimum–maximum) determined for 48 stream and river sites in Puerto Rico where American eels were collected 2005–2016

Percent land cover or ownership	Mean	*SD*	Min–Max
One hundred meter riparian			
Agriculture	21.73	14.35	0.20–57.30
Forest	63.20	21.25	28.80–99.00
Shrub and woodland	10.10	6.86	0.70–28.10
Urban	4.56	8.27	0–34.30
Private	77.46	30.55	0–100.00
Public	22.18	30.80	0–100.00
Utility and NGO	0.37	1.13	0–4.70
Watershed			
Agriculture	30.63	19.02	0.30–67.90
Forest	54.39	25.82	12.40–99.00
Fresh water	0.19	0.35	0–1.60
Shrub and woodland	10.03	6.92	0.60–27.90
Urban	4.57	8.67	0–39.40
Private	76.81	31.51	0–100.00
Public	22.91	31.65	0–100.00
Utility and NGO	0.26	0.80	0–3.40

3.4 | Stressors, threats and impacts

As with most fisheries and ecosystems, the ultimate driver regulating system integrity and productivity is the human population — and this is especially true in Puerto Rico, which has an extremely dense population. The Caribbean region is among the most densely populated areas globally, and Puerto Rico is among the most populated islands (United Nations 2014). The Puerto Rico population has fluctuated dramatically for the last decade, peaking in 2009 at just under 4 million people, and decreasing steadily since. With conflicting uses of natural resources, aquatic ecosystem and fisheries management is a balancing act between meeting human water needs and maintaining the integrity of ecosystems and sustainability of fisheries (Engman & Ramírez, 2012; Kwak & Freeman, 2010; Neal et al., 2009).

The stressors and threats to the American eel in the Caribbean are similar to those in its northern, temperate distribution (Shepard, 2015), however, some human impacts to the species are realised and active, while others remain impending and are not fully understood. Those realised include dams and other migratory barriers, habitat loss and alteration, and pollution; those impending span exotic species and commercial harvest; and the least understood is climate change.

Dams and other barriers to migration are by far the most critical stressor and limitation to the American eel in Caribbean fresh waters. All native freshwater fish species in Puerto Rico are diadromous (most are amphidromous) and depend on connectivity between freshwater and marine habitats. Dams and instream barriers block the fish migrations required to complete their life cycle and lead to local and widespread extirpations (Figure 5; Cooney & Kwak, 2013; Greathouse, Pringle, McDowell & Holmquist, 2006; Holmquist, Schmidt-Gengenbach & Yoshioka, 1998). By integrating the Puerto Rico island-wide fish surveys with those for dams and instream barriers, a barrier height of 3.0 m (2.0–4.0 m 95% prediction interval) was identified as a critical threshold for blocking American eel migration, and no American eel was detected upstream of a barrier greater than 2.5 m high (Figure 5; Cooney & Kwak, 2013). When barrier heights exceed 4.1 m, all non-goby native fishes are blocked from upstream migration, and high dams exceeding 31.9 m high block all native fish species migration. For the American eel in Puerto Rico waters, this results in effective extirpation of the species from 38.9% of river length islandwide, due to upstream river reaches blocked by instream barriers (Figure 6). Furthermore, the fish assemblages in reservoirs upstream of high dams are dominated by exotic species, which may create a predator gauntlet for any American eel able to ascend migratory barriers (Cooney & Kwak, 2013; Johnson, Olden & Vander Zanden, 2008). This extirpation from upstream, high-elevation stream reaches may be especially detrimental to the American eel in Caribbean streams, where upstream habitat may be important for females.

Habitat loss and alteration in addition to that resulting from dams and barriers is a presumed limitation to American eels in Caribbean waters. Hierarchical models to describe Puerto Rico fish assemblage

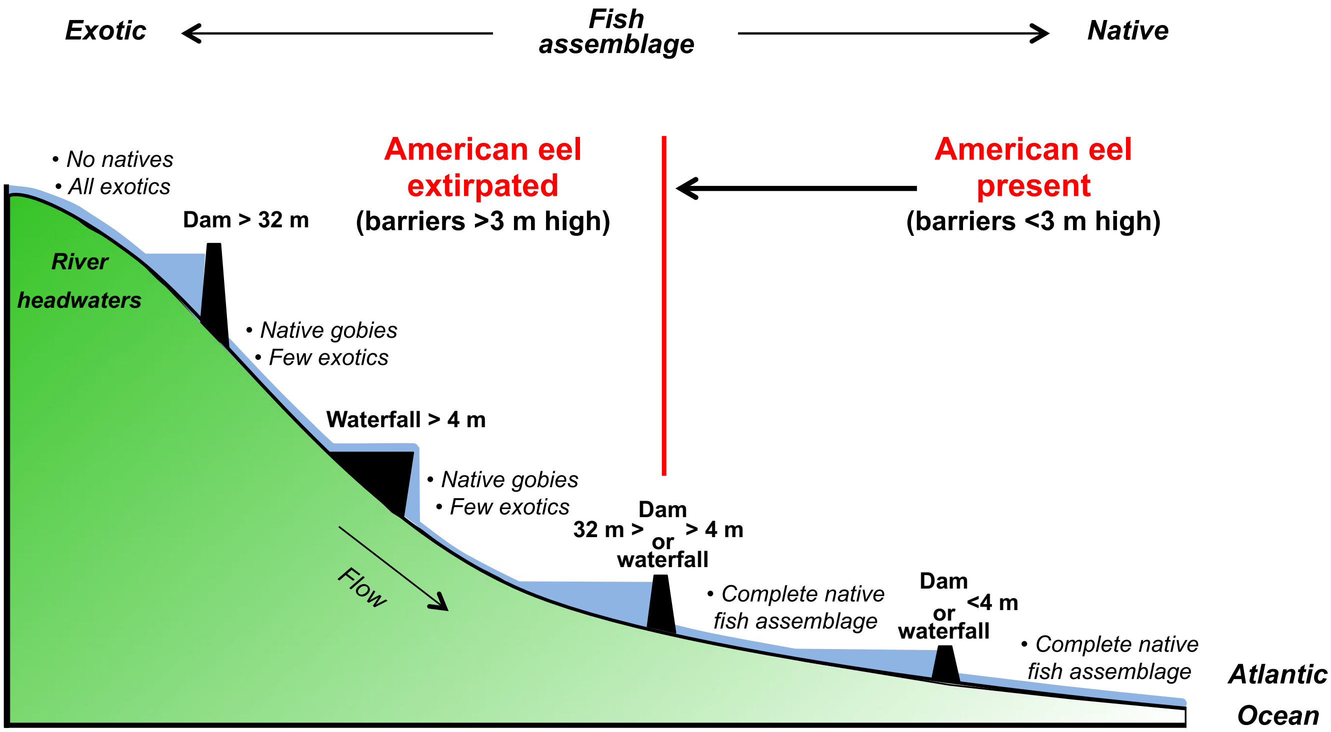


FIGURE 5 Instream barriers are a primary factor affecting the habitat availability and distribution of the American eel in the Caribbean region and form a continuum in the fish assemblage from native to exotic species proceeding upstream. Barriers higher than 3.0 m effectively block the upstream migration of American eel, rendering any upstream habitat unavailable (Cooney & Kwak, 2013) [Colour figure can be viewed at wileyonlinelibrary.com]

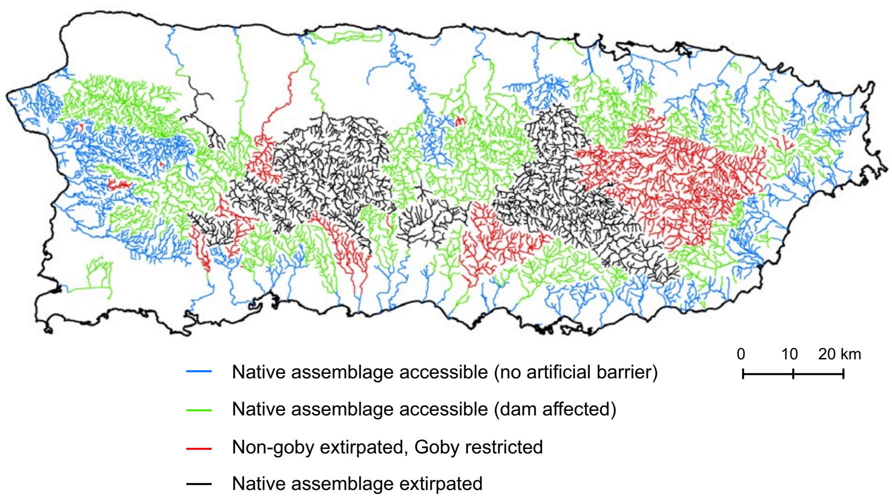


FIGURE 6 The American eel (and all nongoby native fishes) is effectively extirpated (5% estimated occurrence) from 38.9% of river length by instream barriers in Puerto Rico (red and black lines). A vast majority (74.5%) of river length is affected by instream barriers (green, red, and black lines), and all native diadromous fishes are extirpated from 21.6% of river length (black lines; Cooney & Kwak, 2013) [Colour figure can be viewed at wileyonlinelibrary.com]

patterns from instream habitat parameters and landscape attributes revealed that basin-level influences appear to structure fish assemblages more than site- or reach-scale factors (Kwak et al., 2007, 2013). However, American eel was extirpated from stream reaches with extreme habitat alteration (i.e. concrete-lined and channelised) in the urban Río Piedras watershed (Engman & Ramírez, 2012). The tolerance of the American eel to altered stream conditions suggests its distribution is primarily limited by other factors, such as migration barriers, but survival and abundance may be influenced by habitat quality.

Water quality is known to influence fish distribution and abundance, and the fresh waters of Puerto Rico have received substantial sediment, chemical and nutrient pollution from a variety of sources (Hazen, 1988; Hunter & Arbona, 1995; Warne, Webb & Larsen, 2005). However, recent surveys of aquatic contaminant concentrations in Puerto Rico stream and river habitats and biota revealed that the ecosystems were not severely polluted, with the exception of elevated concentrations of nickel, polychlorinated biphenyls (PCBs), and mercury in several fish species from agricultural and urban streams (Buttermore et al., 2018). Elevated PCB concentrations in

American eel (0.019–0.031 ppm wet weight) were high enough in an urban Puerto Rico stream to pose a human health hazard.

Exotic species, including fishes and parasites, are potential threats to the American eel in the Caribbean. The freshwater fish fauna of Puerto Rico is dominated by exotic species, but their impact on native fishes, including the American eel, are minimally understood (Kwak et al., 2016; Neal et al., 2009). The absence of the swim-bladder nematode *Anguillicoloides crassus* in 120 American eels examined suggests a low incidence of the exotic parasite if it is present at all. The pathogenicity and population effects of *Anguillicoloides crassus* on the American eel are not well documented, but damage and pathological effects to the swim bladder are evident, and other health, survival and reproductive impacts are likely (Hein, Arnott, Roumillat, Allen & deBuron, 2014; Kirk, 2003; Shepard, 2015). A suite of other parasites are also known to infect anguillid eels (Cone, Marcogliese & Watt, 1993; Nagasawa & Katahira, 2017; Sures & Kopf, 2004). The prevalence and effects of these parasitic interactions pose a potential threat to the American eel in the Caribbean that is currently unknown.

Commercial fishing for the American eel in the Caribbean has occurred in Cuba, the Dominican Republic and Mexico with variable landings, and glass eel fisheries have been reported in Cuba, the Dominican Republic, Haiti and Jamaica (Benchetrit & McCleave, 2016; Shepard, 2015). American eel were caught and sold in local Puerto Rico fish markets in the early 1900s (Hildebrand, 1935), and small-scale artisanal, subsistence fishing for American eel has occurred since that time. In 2004, all fishing (i.e. commercial or recreational) for American eel early life stages was banned in Puerto Rico. No commercial fishery for American eel exists in Puerto Rico, but illegal fisheries have been detected by Commonwealth authorities, and inquiries to the fisheries agency by prospective fishers are common (personal observation). However, the global demand for cultured and wild-caught eels, their high economic value, and fiscal needs of communities and governments suggest that the potential for commercial harvest in the Caribbean is a serious threat to the distribution and abundance of the American eel in the region.

Climate change has an overarching influence on Caribbean water resources and is an important driver to be considered in conservation planning and policy. In Puerto Rico, precipitation and river flow are projected to decrease in all regions of the island, exacerbating the current water management of this limited resource (Henareh Khalyani et al., 2016; Van Beusekom, Gould, Terando & Collazo, 2016). By contrast, the number and intensity of tropical cyclones has increased with warming sea surface temperature, leading to extreme flooding events (Webster, Holland, Curry & Chang, 2005). If water allocation policy continues to favour human uses over ecological needs, the impact on stream ecosystem services, including fish resources, will worsen and affect the American eel in the region.

4 | CONSERVATION IMPLICATIONS

The research findings presented, placed in a broader perspective with published literature, identify similarities and differences between American eels in the tropical Caribbean environment against those in the temperate Atlantic. The findings on American eel in Puerto Rico substantially expand knowledge of the distribution and abundance, population biology, habitat ecology, and stressors, threats and impacts on the species. Specifically, the resource was quantified, which is the first step for conservation planning, including aspects of size structure and sex ratios. The findings on migration barriers elucidate the mechanisms and extent of blocked stream passage and suggest that upstream, high-elevation habitats that may favour female eels are important, but limited habitats. The threat assessment of realised, impending and poorly understood stressors further highlights similarities and differences between tropical and temperate American eel segments and can serve as a basis for conservation planning and actions. A common theme in this synthesis is that many aspects of American eel biology and ecology are not well researched or understood, and this is especially true for the species in the Caribbean. There is a need for continuing research on this important, but enigmatic species to guide conservation and management of the American eel based on the best available science.

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