A NOVEL METHODOLOGY FOR SPATIAL ANALYSIS OF THE CONSERVATION STATUS OF THE AMERICAN EEL (*ANGUILLA ROSTRATA*) OVER LANDSCAPE SCALES

by
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DEDICATION

Dedicated to the citizens of Eel Town. Please join us at www.EelTown.org.

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I thank my family for their support during this process. James Prosek for his book and documentary on American Eel and advice during the beginning part of this project. The commercial fishers, tribal fishers, eel dealers and state agency representatives who helped provide data for Chapter Two. Erik Martin at The Nature Conservancy for advice on studies of fish habitat prioritization. Aaron Bunch at the Virginia Department of Game and Inland Fisheries, Keith Whiteford and Jim Thompson at Maryland Department of Natural Resources, Andy Dolloff at the U.S. Forest Service and Sheila Eyler at the U.S. Fish and Wildlife Service for help finding biological data. Kirby Rootes-Murdy and Kristen Anstead at the Atlantic States Marine Fisheries Commission, Steven Shepard at the U.S. Fish and Wildlife Service, Sara Rademaker at American Unagi and Chris Bowser at New York State Department of Environmental Conservation for feedback on various sections. Sally Evans at University Thesis and Dissertation Services for reviewing the formatting of this manuscript. Sheryn Reid for the Eel Town artwork. To all the members of Eel Town around the world.

Thank you to everyone who helped make this possible.

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LIST OF ABBREVIATIONS

Atlantic States Marine Fisheries Commission .... ASMFC
Advanced Spaceborne Thermal Emission and Reflection Radiometer .... ASTER
Catch per sampling event .... CPSE
Catch per unit effort .... CPUE
Committee on the Status of Endangered Wildlife in Canada .... COSEWIC
Dichlorodiphenyltrichloroethane .... DDT
Digital Elevation Model .... DEM
Diel Vertical Migration .... DVM
Endangered Species Act .... ESA
Fisheries Management Plan .... FMP
International Union for Conservation of Nature .... IUCN
Department of Marine Resources .... DMR
Department of Natural Resources .... DNR
National Oceanic and Atmospheric Administration .... NOAA
Polycyclic aromatic hydrocarbons .... PAHs
Polychlorinated biphenyls .... PCBs
Polychlorinated dibenzodioxins .... PCDDs
Polychlorinated dibenzofurans .... PCDFs
Single Nucleotide Polymorphism .... SNP
Traditional Ecological Knowledge .... TEK
U.S. Department of Justice .... DOJ
U.S. Fish and Wildlife Service .... USFWS

ABSTRACT

A NOVEL METHODOLOGY FOR SPATIAL ANALYSIS OF THE CONSERVATION STATUS OF THE AMERICAN EEL (ANGUILLA ROSTRATA) OVER LANDSCAPE SCALES

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George Mason University, 2019

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The American Eel (*Anguilla rostrata*) was the most numerous fish on the Atlantic Coast but the population has been reduced from pristine levels as a result of overfishing, dams, pollution, invasive parasites and other factors. I present a work in four sections to provide a roadmap for restoring this species and habitat. Chapter One provides the most recent literature review on the species, including an overview of the anthropogenic factors affecting the population and potential mitigation measures. Chapter Two is a study of the American Eel fisheries in Maine and South Carolina based on published data and interviews with state agencies, commercial fishers, exporters and tribal fishers. Chapter Three is a compilation of data on American Eel in the mid-Atlantic region from 1911 to 2018, with records >3.75 million individual fish and a discussion on eel demographics over time and space. Chapter Four builds upon the dataset in Chapter Three to create a map of the watersheds of the Chesapeake Bay in ArcGIS to study the effects of dams and land use

on eels. Results indicate American Eel are limited by dams and barriers blocking access to habitat, as evidenced by the high numbers of eels on the lower James and York rivers but much lower numbers upstream. It is difficult to draw conclusions however because of limitations in the datasets. The database is the largest of its kind, combining several biological and ecological factors and the GIS model presents a novel method for studying watersheds and migratory ichthyofauna.

CHAPTER ONE: LITERATURE REVIEW OF THE AMERICAN EEL (*Anguilla rostrata*) IN THE U.S. AND AN OVERVIEW OF CONSERVATION PRACTICES

ABSTRACT

This paper presents the first review of American Eel (*Anguilla rostrata*) since 2015. It incorporates the latest knowledge on biology and ecology. This includes the eel lifecycle from larvae to spawning, the three life strategies (freshwater, brackish water and saltwater), habitat use and migration. I summarize recent scientific research since the last review including the American Eel genome and the first mapping of the downstream migration route. I discuss anthropogenic stressors such as dams, pollution, parasites, habitat degradation, fishing, climate change, changes to the Sargasso Sea and aquaculture, as well as some proposals for mitigation. Finally, I discuss citizen science, education and outreach activities.

INTRODUCTION

The genus *Anguilla* was described by Schrank in 1798, with the last review by Lecomte-Finiger in 2003. Eels evolved about 200 mya (Als et al., 2011) and current taxonomy based on phylogenetics documents 19 species. The American Eel (*Anguilla rostrata*) is widely distributed from Greenland, Canada, the eastern United States, Mexico, Central America, many Caribbean islands with freshwater lakes and streams (as far south and east as Trinidad) and in South America drainages in Colombia, Venezuela, Guyana, Suriname, French Guiana and northern Brazil (Benchetrit & McCleave, 2015).

The last comprehensive review of American Eel was published by the U.S. Fish and Wildlife Service (USFWS) in 2015 (Shepard, 2015b). Since then, scientific research has progressed in a variety of areas. For example, in 2016, the American Eel migration route from Canada to the Sargasso Sea was mapped using satellite tags. This route shows two phases of migration, one along the edge of the continental shelf and the second in deeper waters straight south toward the spawning area (Béguer-Pon et al., 2016).

The American Eel genome was sequenced in 2017 (Pavey et al., 2017) and is available in GenBank (accession LTYT01000000). While the entire American Eel spawning stock is one large population, there is evidence of gene and environment interactions at the gene expression level among riverine systems, supporting the concept of different ecotypes (Gaillard et al., 2018) that have been observed using candidate genes in eels from the St. Lawrence Estuary and Nova Scotia. For example, glass eels from the St. Lawrence estuary have a greater capacity to use lipid reserves to sustain their metabolic needs. This supports observations of regional phenotypic variation in American Eel being determined early in life (Gaillard et al., 2016).

Panmixia means the genes of individuals from freshwater, saltwater and brackish water habitats are all mixed at spawning time. But individuals may still segregate to different locations based on intra-generational spatially variable selection, which has been observed in both American and European Eels. Based on SNP analysis, there are hundreds of genes at play and not simply one switch gene that changes the eels from a saltwater to freshwater ecotype (Pavey et al., 2015). One gene that may play a role in the ecotype adaptation is Urinary transporter 2 (Ut2). This gene may be necessary for the eel to cross from saltwater to freshwater and is associated with the freshwater ecotype. Additional genes related to heart development may play a role during migration, as the freshwater ecotype has an additional 1,300 km to travel (Trancart et al., 2014).

The freshwater ecotype has a different growth and reproductive strategy than the brackish and saltwater ecotype. The eels that remain in salt and brackish water tend to grow quickly and migrate back to the Sargasso Sea as soon as possible to reproduce. This makes sense for a reproductive strategy where the costs of waiting to reproduce do not outweigh the benefits of increased fecundity, which is the case for males. On the other hand, female eels have adapted a bimodal strategy, where some remain in brackish or saltwater and reproduce after ~5 years while others migrate toward freshwater, grow to large size and wait >20 years to reproduce (Pavey et al., 2015). Since this latter ecotype is more fecund than smaller females and can make a greater contribution to the population, this ecotype is very important for conservation efforts, which are compounded by its much longer migration route (often over 1000 km) to reach the Sargasso Sea.

In spite of panmixia, there are two possible genetic mechanisms that could create differences each generation and result in the observed phenotype plasticity. One is genotype-dependent habitat selection and the second is intra-generational spatially variable selection. The first hypothesis is supported by the evidence that glass eels make choices based on salinity differences in controlled settings (Edeline et al., 2005). If the choice groups can be differentiated genetically, it would result in genotype-dependent habitat segregation. The second hypothesis is supported by studies of both American and European Eels. Differences in salinity, biotic interactions and flow regime in the studied ecotypes may represent stronger selection, indicating spatially variable selection on the freshwater-saltwater axis (Pujolar et al., 2014).

Phenotypic differences have been identified using head shape morphology for both European and Japanese Eel (Appelbaum & Riehl, 1993; Barry, 2015; De Meyer, Jens et al., 2016; De Meyer, J. et al., 2015; Ide et al., 2011; Proman & Reynolds, 2000), but I am aware of only one study examining head shape morphology (among other factors) in American Eel (Cottrill et al., 2002). Since there is continued debate about what drives the differences in head shape, e.g. is it determined by diet, environment or selection within streams, these data could provide additional tools for conservation at local scales. In European Eel, a broad head shape is linked to being more piscivorous and a higher incidence of *A. crassus* infections (Pegg et al., 2015).

Research is also taking into account cultural science, the ways humans interact with eels in the present day as well as historically (Tsukamoto, 2014). Traditional Ecological Knowledge (TEK) is being incorporated into eel management, see (Giles et al., 2016).

LIFE CYCLE AND MIGRATION

Despite considerable advances, details of American Eel at each life stage remain limited. Both American and European species spawn in the Sargasso Sea near Bermuda, although no one has witnessed this behavior in the wild (Bertness et al., 2013). The Sargasso Sea is unique in that it is the only place in the world with holopelagic *Sargassum*, which provides food for eel larvae (Kuroki et al., 2017). Based on mtDNA, the timing of evolutionary divergence of American and European Eels was 3.38 mya (Jacobsen et al., 2014) as result of Pleistocene climate cooling (Lecomte-Finiger, 2003). Despite this, there is no evidence of hybridization other than very few putative hybrids found in Iceland (Als et al., 2011). The eel lifecycle is shown (Fig. 1).

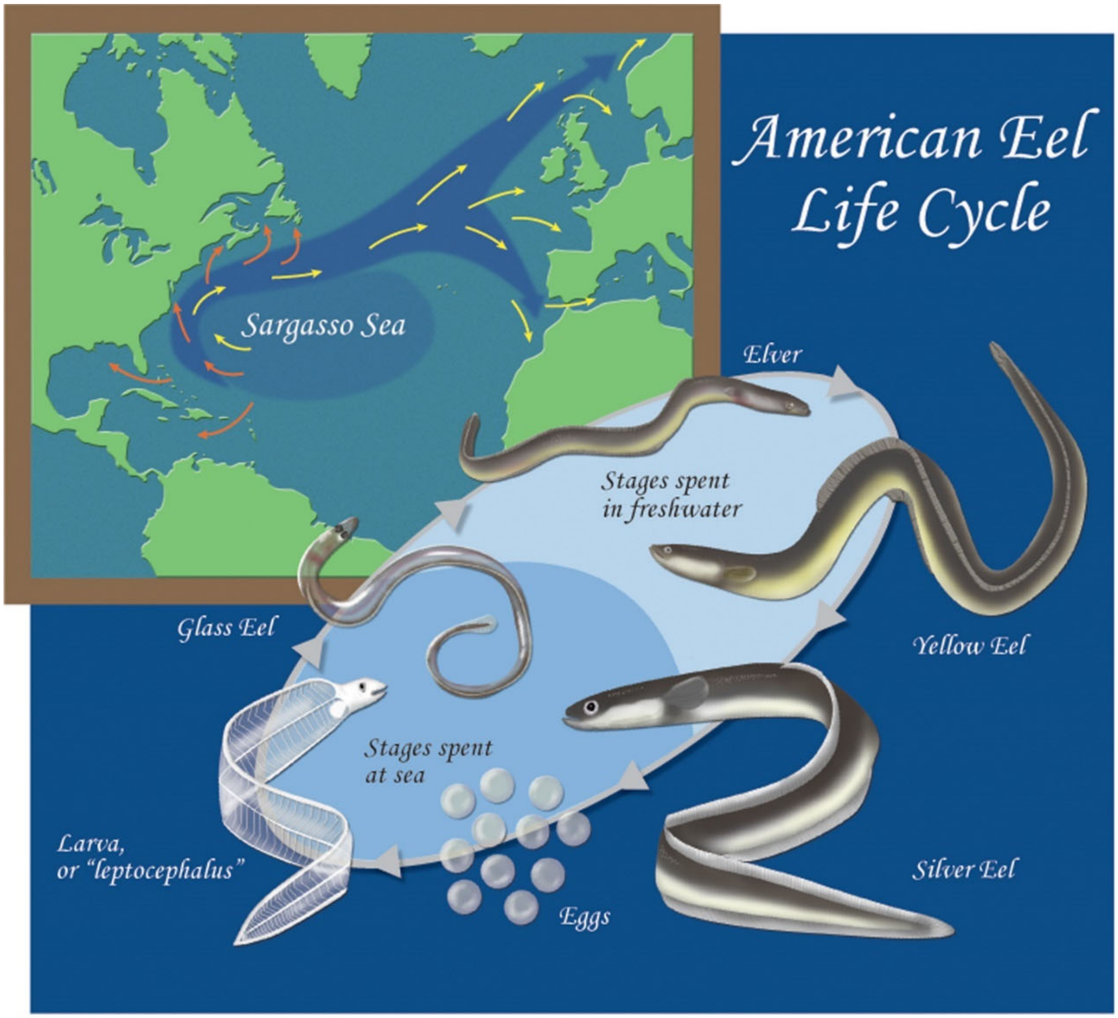

Fig. 1. Each stage of the lifecycle of the American Eel (*Anguilla rostrata*). Spawning occurs in the Sargasso Sea, where eggs hatch into leptocephali (larvae) and migrate to coastal waters of North and Central America. At coastal rivers, they metamorphose to elvers (that develop into yellow stage eels) that migrate into streams and estuaries before maturing to silver eels. Life stages are not to scale. Illustration © Melissa Beveridge (Beveridge, 2009). Used with permission.

Most American Eels are catadromous, spending the majority of their lives in estuarine and riverine environments before returning for spawning at sea, the opposite of salmon and many other aquatic organisms. American Eel cover a broad geographic range while maintaining intraspecific panmixia (Avise, 2011; Velez-Espino & Koops, 2010), i.e.

all individuals are potential partners and all recombination is possible (Als et al., 2011). Because of this, the entire American Eel population is homogenous.

Anguillid species are sexually, ecologically and behaviorally highly adaptive (McCleave, J. D., 2001). Eels are found in higher diversity of habitat than any other fish, from oceans to estuaries to lakes and rivers (Helfman et al., 1987), the result of adaptability during feeding and growth (juvenile) stages in continental waters (Jessop, 2010). The spawning and larval stages require very specific marine habitat conditions, which may make them susceptible to changes in climate and ocean currents (Shepard, 2015b). Based on genetic parameters, between 50 and 100 million eels congregate to spawn in the Sargasso Sea each year (Cote et al., 2013). American Eel spawn from February to April, overlapping slightly with the European Eel, which spawns from March to May. Geographically, the two species spawning grounds overlap slightly in the middle. Based on temperature and salinity gradients, both American and European Eels likely spawn in upper 300 m of the ocean (Tesch, 2003).

After spawning, the non-sexually differentiated larvae, called leptocephali, drift toward Atlantic coastal waters via the Gulf Stream (Lecomte-Finiger, 2003; Shepard, 2015b). Dispersal is apparently random but American Eel use diel vertical migration (DVM) to detrain themselves from the Gulf Stream and separate from the migration patterns of European Eel (Ginneken & Maes, 2005; Velez-Espino & Koops, 2010). The gut contents of eel larvae in the Sargasso Sea have been studied using high-magnification microscopy, which shows the presence of multiple size ranges of marine snow particles, containing a wide variety of components likely related to bacteria, protists, fungi, or other organisms (Miller et al., 2019).

Larvae metamorphose to glass eels upon reaching or coastal, brackish, or fresh waters (Lecomte-Finiger, 2003). Glass eels move extensively in continental shelf waters for several years, with time varying by geography and other factors. Glass eels require 60-110 days to swim from gulf stream to the east coast of North America (Powles & Warlen, 2002; Wuenschel & Able, 2008). Arrival occurs during winter and spring, beginning in the south and proceeding northward (Helfman & Bozeman, 1984; McCleave, J. D. & Kleckner, 1982). Glass eels begin to transform into pigmented elvers within days of arrival in coastal waters. As they continue moving into rivers, they complete the transformation to become elvers (Lecomte-Finiger, 2003).

Colloquially, “glass eel” and “elver” are often used interchangeably, but these terms are not biologically synonymous. The glass eel stage begins when the leptocephali metamorphose to an eel-like but transparent body morphology, while elvers are pigmented and longer. The variability in size reflects the fact that the term “elver” may include several age classes, with first-year elvers called young-of-the-year (YOY). YOY are sampled annually at various sites because this is the one time when it is possible to determine that all of the eels are from the same cohort (ASMFC, 2000a). Elvers grow into the yellow eel stage, which can last anywhere from 3 to 30 years or more, with females silvering at later ages and mean age increasing with latitude (Helfman et al., 1987; McCleave, J. & Edeline, 2009).

A large portion of the eel life cycle takes place in the yellow phase, when some individuals migrate upstream toward headwaters (Welsh & Liller, 2013). American Eel was once thought to be an obligatory catadromous species. Recent studies using strontium to calcium concentrations (Sr:Ca) in otoliths, which differ based on time spent in saltwater and freshwater, have challenged this hypothesis (Jessop et al., 2002; Lecomte-Finiger, 2003; McCleave, J. & Edeline, 2009; Velez-Espino & Koops, 2010).

After elvers arrive in coastal waters, they may adopt one of three strategies (as well as intermediate approaches) during the growth (yellow eel) phase: The first strategy is to remain in the lower estuary and coastal habitats (sometimes remaining exclusively in marine waters). The second, called amphidromy, is to adopt semi-catadromous behavior by remaining in brackish waters and the third is to exhibit catadromous behavior by moving into lakes and rivers (Arai & Chino, 2012; Jessop et al., 2002, 2006). This mix of migratory strategies has been observed in European and Japanese Eels as well (Lamson et al., 2006; Thibault et al., 2007b; Velez-Espino & Koops, 2010; Zhu et al., 2013).

Variations on these migratory themes are found across a wide geographic area. In Nova Scotia, thousands of yellow eels migrate downstream to estuaries in spring and back upstream in winter. Similar behavior is observed in the St. Jean River, where some eels move downstream in the spring to exploit the superior feeding opportunities in the estuary, as evidenced by gut contents from analyzed fish. The estuary may be inhospitable during winter as eels, like most fishes, do not have antifreeze proteins, further evidencing that migration likely evolved in warmer environments (Thibault et al., 2007a). In the East River (Nova Scotia), the Hudson River Estuary (Velez-Espino & Koops, 2010), the York River

(Hedger et al., 2010) and near Prince Edward Island on the Gulf of St. Lawrence (Lamson et al., 2006), some yellow eels overwinter in freshwater habitats while migrating short distances to feed in estuaries or marine environments. That not all fish migrated to or stayed in one location shows both habitats are viable habitats for summer survival (Hedger et al., 2010).

Since migration is not obligatory, the reason for migrating is not clear. Catadromous behavior may have evolved if the gain in food abundance in estuaries outweighed the costs of migration (Arai & Chino, 2012), plus movement between fresh and saltwater could be in response to low winter temperatures (Thibault et al., 2007a).

Extended time in freshwater however increases vulnerability from fisheries and bioaccumulation of contaminants (especially lipophilic contaminants affecting reproduction and early embryonic development) (Lamson et al., 2009), but these are relatively recent phenomena and not tied to the evolutionary history of Anguillid eels. In fact, use of freshwater by eels is paradoxical since they grow faster in saltwater habitats. American Eel double their growth rate in brackish water (unlike European, Japanese and Australian Eels, which only grow 13% faster in saltwater). Widespread freshwater migration may also be a sign that the large population is unable to adapt to local conditions, as migration appears to be most beneficial in tropical environments (Cairns et al., 2009). The different strategies may also be a response to local population densities, since eels are able to rapidly colonize or occupy habitat across a broad spectrum of physical and chemical conditions to reduce competition or risk of predation (Shepard, 2015b).

Yellow eel maturation varies by sex and location (faster for males and faster in tropical waters) with some yellow eels able to move between freshwater and estuarine systems for feeding (Hansen & Eversole, 1984). The disparity in times is due to varying methods of estimation and increasing time to maturation from Southern to Northern latitude. Yellow eels are opportunistic feeders, consuming nearly any live prey that can be captured. Smaller eels eat benthic invertebrates, larger eels consume mussels, fish and even other eels. They adapt to seasonal prey availability, decreasing intake or ceasing to eat during winter and will respond to local abundances of prey (Tesch, 2003).

Estuaries provide abundant food, hence the highest yellow eel growth rate (Fenske et al., 2010) although rates are highly variable. Estimates from wild-caught American Eel indicate a higher mean growth rate for females (53 mm/year) than for males (26 mm/year). Males metamorphose at a smaller size (between 328 and 392 cm) than females (404–1016 cm) and earlier (5.3–15.4 vs 5.8– 21.5 years) (Jessop, 2010).

Although yellow eels are habitat generalists, they have size-specific substrate preferences (Dutil et al., 1988; Oliveira & McCleave, 2000). As young eels grow, density dependent competition prompts them to disperse into generally less crowded upstream habitats. Larger eels tend to occupy slow moving, deep water habitats compared to their smaller conspecifics (Wiley et al., 2004).

American Eels tend to be nocturnal, sheltering during daylight hours (Welsh & Liller, 2013), a behavior consistent across the genus (Hedger et al., 2010). In the York River Estuary, American Eel exhibit selective tidal stream transport (STST) generally traveling upstream from early to late evening and downstream from late to early morning, coincident with tidal movement (Welsh & Liller, 2013). In estuaries, most sightings are associated with eelgrass *Zostera marina* L., which provides cover and foraging opportunities. The smallest American Eel are most selective of habitat (Thibault et al., 2007a).

Sex ratios of American Eel populations can be highly variable, with 90% of eels being males or females depending on the locality (Goodwin & Angermeier, 2003), with higher percentages of males found in higher salinity waters (Velez-Espino & Koops, 2010). As size is linked to fecundity (fitness) for females but not males, females take longer to mature they are generally larger and older at spawning time (Hamilton, 1967; Velez-Espino & Koops, 2010).

Female eels more common in north and in habitats where density is low. Males tend to grow fast, mature early at small size, females tend to grow more slowly and mature at much later age and larger size. Life history plasticity observed among the diversity of habitats may be an adaptive mechanism that optimizes female growth and egg production while minimizing investment in male growth. As eel density decreases, female proportion increases. This could be a compensatory behavior to shift sex ratios during times of low abundance. Mean density decreases by an order of magnitude with distance inland from the coast, mean biomass declines by only 50% because of larger size and relative fecundity of female eels (Shepard, 2015b).

Ultimately, yellow eels metamorphose again to become silver eels, before returning to the Sargasso Sea to complete their life cycle. The onset of migration is likely triggered and synchronized by temperature and salinity (Shepard, 2015b; Verreault et al., 2012).

Although never documented in the wild, silver eels appear to die after spawning (Helfman et al., 1987). Prior to metamorphosis, eels are intersexual (McCleave, J. D., 2001). Sexual differentiation takes place during a second metamorphosis to silver eels (Velez-Espino & Koops, 2010) although yellow eels > 40 cm are traditionally sexed as female (Dolan & Power, 1977). In some cases (e.g. low fat content, higher temperatures, or inability migrate downstream), eels can revert from the silver stage to yellow eels if unable to migrate downstream (Shepard, 2015b; Verreault et al., 2012).

The year an eel migrates downstream is more dependent on sex-specific length than absolute age, with differences in growth and migration reflecting an evolutionary stable strategy adaptable across a wide range of habitats (Velez-Espino & Koops, 2010). Male fitness is maximized by maturing at the smallest size that allows a successful spawning (time-minimization strategy). Female fitness appears to optimize the risk of pre-reproductive mortality with greater fecundity by older (presumably larger) individuals, with a bimodal size distribution has been documented for female silver eels (Davey & Jellyman, 2005). Gender distribution is determined by habitat characteristics, such as relative proportion of lake versus stream habitat, latitude, salinity, productivity (Cote et al., 2009) and demographic attributes such as eel density, growth rate, age at maturity, length and weight (Fenske et al., 2010; Oliveira & McCleave, 2000). This variation in age at maturation increases reproductive success by individuals of a particular cohort as it is more likely that at least some will find favorable spawning conditions (Shepard, 2015b).

ANTHROPOGENIC IMPACTS ON AMERICAN EEL

DAMS

Dams affect both upstream and downstream movements, migration patterns and timing, stream network connectivity (Verreault et al., 2012), restrict the range where eels can live (Hitt et al., 2012), reduce indigenous aquatic fauna and alter riparian vegetation through inundation, flow alterations and influences on groundwater and the water table (Gregory et al., 2002). On the Hudson River, eel density upstream of natural and artificial barriers was reduced by at least a factor of 10 with significantly lower biomass (Machut et al., 2007; Schmidt et al., 2009).

Standing water (lacustrine) habitat found in lakes, reservoirs and wetlands is considered among the most important habitat for eel because lake habitats primarily produce large, highly fecund, female eels, particularly at northern extremes of the range (Castonguay et al., 1994). Dams replace lotic habitat with lentic habit (going from flowing to non-flowing) (McCleave, J. D., 2001).

But the loss of fluvial habitats because of barriers has negatively affected American Eel (ASMFC, 2000b), distribution and abundance. Most of the loss of access to rivers occurred prior to 1960 (Shepard, 2015b) although construction continued after that time (Conservancy, 2019). The effect of dams on upstream eel migration varies by site. Some may be complete barriers or may restrict eels of certain sizes, or may block eels only during specific flow conditions (Acou et al., 2008).

Upstream passage facilities (lifts, ramps, fishways) built specifically for elver and yellow stage eel are becoming more common, usually with a sloped ramp with pegs or a rough substrate (Shepard, 2015b). Fishways can be effective. for example, in 1997 the eel population at the foot of Lake Champlain's Chambly Dam was estimated at 19,650 individuals, with minimum ladder efficiency estimated at approximately 57 to 68 %. This ladder re-established historic eel access to 120,000 ha of habitat (Verreault & Dumont, 2003). Eels can pass through various fishways but usually only at larger size.

Hydroelectric dams delay migration and cause mortality, which can cause silver eels to revert to the yellow eel stage if they encounter obstacles or delays (Winter et al., 2007). Turbines can also decrease local and regional abundance and skew population toward smaller and younger females, and more males (Shepard, 2015b).

There are a variety of methods to help silver eels safely get downstream, including trap and transport programs and fish screens to divert eels toward bypass chutes. In a study on the impacts of five hydroelectric dams on the Shenandoah River, 2/3 of migrating silver eels used the spillway and the other 1/3 went through the turbines, with pass via spillover more common during times of high river discharge. Turbine mortality ranged from 15.8% to 40.7% at individual dams (Eyler et al., 2016). On this river, a shutdown from 1800–0600 hours protected 81% of downstream-migrating eels, with 50% percent of downstream passage events occurred between September 15 to December 15. There is variability in the migration time and additional dates of turbine shutdowns could protect more migrating eels (Eyler et al., 2016).

Dams that are nonfunctioning, causing environmental harm or unsafe conditions may be considered for removal. Many dams were built long ago and are no longer needed (Welsh & Liller, 2013). Several methods exist for determining the best candidates for removal. For migratory fish, removing the dam furthest downstream may provide the best return on investment. As eels in temperate regions have a greater chance of remaining in lower reaches of brackish water, dam removal could be prioritized in tropical areas (Velez-Espino & Koops, 2010). Dam removal has also been done according to the Habitat Suitability Index (HSI) model for diadromous fishes (Kocovsky et al., 2009; Kocovsky et al., 2008). Another option to justify dam removal is to weigh the benefits (e.g. hydropower) against the costs of fish ladders or transporting fish by barge as well as the loss of ecosystem services provided by fish and other fauna (Sekercioglu, 2010).

One example of the services provided by eels is the distribution of the larvae of freshwater mussels (Bivalvia: Unionidae), which are host-dependent and attach to fish hosts until they become free-living juveniles (Galbraith et al., 2018). The eastern elliptio mussel, *Elliptio complanata*, uses American Eel as its primary fish host, but both species are in decline (Strayer & Malcom, 2012). These mussels are declining and disappearing from many waters around the world, often because of failing recruitment rather than adult mortality. With dams cutting off eel mobility, mussels lost their distribution system as well. In the Chesapeake Bay watershed, *E. complanata* recruitment is limited and appears to be linked to host species distribution, since the mussels are much more abundant downstream of dams on the mainstem of the Susquehanna River than upstream (Galbraith et al., 2018). Considering that in the Delaware River, these mussels once filtered two billion gallons of water per day (Prosek, 2011), by restoring fish passage and habitat there is the potential to improve water quality as well.

Dam removal prioritization depends on biological, social and economic factors. Dam removal will also result in hydrologic changes both up and downstream, such as sediment movement and deposition, which alter fine-scale habitat suitability (Kocovsky et al., 2009). Because of these changes, pre-removal risk assessments must be conducted especially in areas where upstream sediments contain pollutants (Gregory et al., 2002).

Regardless of the criteria used dam removal has been successful in restoring ranges of American Eel. When the Ft. Edward Dam was removed from the Hudson River, eels were observed in upstream habitats that had been inaccessible for 150 years (Hart et al., 2002). Eel abundance also increased significantly after the Embrey Dam in Fredericksburg Virginia was removed in 2004. This dam appeared to have been preventing the migration of smaller individuals and its removal increased eel abundance up to 150 km upstream in less than a year (Welsh & Liller, 2013).

Although dam removal may be a good way to restore eel range and habitat, it is sometimes expensive and difficult. Eel ladders are relatively cheap and can provide passage quickly although they may not be ideal for all fish (Schmidt et al., 2009). An eel ladder retrofitted to a dam on the Shenandoah River is accessible to eels between 19 to 74 cm in length. It appears smaller eels are not able to ascend, but most in that size range have probably not yet metamorphosed to yellow eels and therefore are not migrating upstream (Welsh & Liller, 2013).

POLLUTION

Eels, especially females, encounter a variety of pollutants along their diverse habitats and long life (Shepard, 2015b). PCBs, PAHs, PCDDs, PCDFs, DDT, heavy metals (e.g. mercury), and other pesticides have been found in yellow and silver eels (Byer et al., 2014). Pannetier et al. (2016) measured the concentrations of essential (Cu, Se and Zn) and non-essential (Ag, As, Cd, Cr, Hg, Ni and Pb) metals in the liver, kidney and muscle tissue of eels sampled at four sites in Eastern Canada. Tissue concentrations of Cd, Hg and Se increased with fish size and age. Tissue metal concentrations of Ag, As, Cd, Cu, Hg, Pb and Se reflected the contamination of their sampling sites. At the concentrations found, the concentrations of these metals (other than As) can pose a risk to eel health (Pannetier et al., 2016).

In the Savannah River in South Carolina, American Eel had the highest cadmium concentrations of any fish sampled (Burger et al., 2001). In the St. Lawrence River, eels contaminated with organochlorine compounds had higher rates of disease and reproductive impairment (Couillard et al., 1997). Chemical pollutants that affect olfactory sense could impact migration, as studies of American Eel rendered anosmic by experiments had difficulty determining the appropriate tide for transport and home site location, although this is not the only mechanism for migration (Barbin, 1998). Urbanization can change the riparian zone affecting shading, allochthonous inputs, hydrology, water chemistry (by altering stream geomorphology) water quality and invertebrate prey densities (Machut et al., 2007).

Contaminant concentrations are consistent with those found in other fish species, but eels survive contaminant loads that would be toxic to other fish (Shepard, 2015b). The unique life history of eels makes it difficult to draw comparisons from other species. Contaminants may have cumulative effects, especially when combined with dietary deficiencies and disease (Arkoosh et al., 1998; Johnson, L. L. et al., 1998).

PARASITES

American Eel can be parasitized by a variety of freshwater parasites including species of Myxoza, Monogenea, Cestoda, Nematoda and Acanthocephala (Shepard, 2015b). *Pseudodactylogyrus bini* and *P. anguillae* are parasitic flatworms that can infect the gills of American and European Eels. The parasite of most concern however is *Anguillicoloides crassus* (Johnson, J. H. & Nack, 2013), a highly infectious nematode that infects the swim bladder of Anguillid eels, causing hemorrhagic lesions, fibrosis and swim bladder collapse (Fries et al., 1996). The Japanese Eel is the traditional host and does not have the same inflammation and pathological changes seen in American Eel (Laetsch et al., 2012) as a result of co-evolution (Knopf & Mahnke, 2004).

Anguillicoides crassus was introduced to Europe in 1982 (Barse & Secor, 1999) and confirmed in North America in 1995 in both Texas and South Carolina (Fries et al., 1996). The wide distribution *A. crassus* has been primarily through anthropogenic means, such as the export of infected eels (Shepard, 2015b). Higher infection rates have also been correlated with urbanized land and higher water temperatures (Machut & Limburg, 2008).

Eggs of *A. crassus* are deposited in the eel swimbladder by the female nematode and develop into second stage larvae that remain within the egg case. Although *A. crassus* has not been found in the early stages of glass eel development, it is found in more advanced stages and fully pigmented elvers. Infection generally takes place within months of arrival into estuaries and generally progresses with eel development (Hein et al., 2015).

Infection rates generally increase with time (Morrison & Secor, 2003). This has been observed in the Chesapeake Bay (Fenske et al., 2010; Moser et al., 2001), as well as in the Hudson River (Machut & Limburg, 2008). Infection rates also vary across watersheds and with salinity gradients (Fenske et al., 2010; Moser et al., 2001), with salinity levels >15 ppt interfering with development and lifecycle completion (Lefebvre & Crivelli, 2012).

HABITAT DEGRADATION AND RESTORATION

Estuarine habitats used by American Eels have been lost because of filling and conversion to upland, as well as eutrophication and contaminants. Nationally, annual rates of estuarine habitat loss are estimated at 0.9%, averaging 2,240 ha per year (Dahl, 2006). Along streams, forest buffers not only reduce run-off from entering streams but also prevent channel narrowing and higher abundances of fish and macroinvertebrates (Sweeney et al., 2004).

Habitat restoration, in the form of riparian buffer zones and estuarine vegetation, can reduce the impact of deforestation, pollution and climate change. Restoring estuarine plants can help slow anthropogenic warming. Saltmarshes, seagrasses and mangroves can sequester more carbon than many terrestrial ecosystems (Fourqurean et al., 2012), since sediment is constantly piling up and does not become carbon-saturated (Day et al., 2012). An increase in riparian buffers can limit eutrophication from run-off and provide cover for juvenile eels that prefer slower depositional areas with deciduous leaf litter for cover (Johnson, J. H. & Nack, 2013).

FISHING

American Eel are harvested at every life stage (Velez-Espino & Koops, 2010). The Atlantic States Marine Fisheries Commission (ASMFC) overseas the American Eel stock in the U.S. According to the 2012 ASMFC stock assessment (and again in the 2017 stock assessment update), eels have declined in recent decades with a significant downward trends in multiple surveys. The ASMFC now considers the American Eel stock depleted (ASMFC, 2012, 2017a). Eels have never been commonly consumed by Americans in modern times, although they were a common food item for Native Americans and early colonists (Giles et al., 2016; Prosek, 2011). Most of the American Eel harvest is exported to Asian markets (Walker et al., 2019).

Fishing catch-per-unit-effort (CPUE) of American Eel began increasing in the 1960s, with peak fishing in the U.S. occurring in 1979 with 1,800 m t and declining in the U.S. and Canada thereafter (Lafontaine et al., 2010; Prosek, 2011; Shepherd, 2006; Verreault et al., 2012) (Fig. 2).

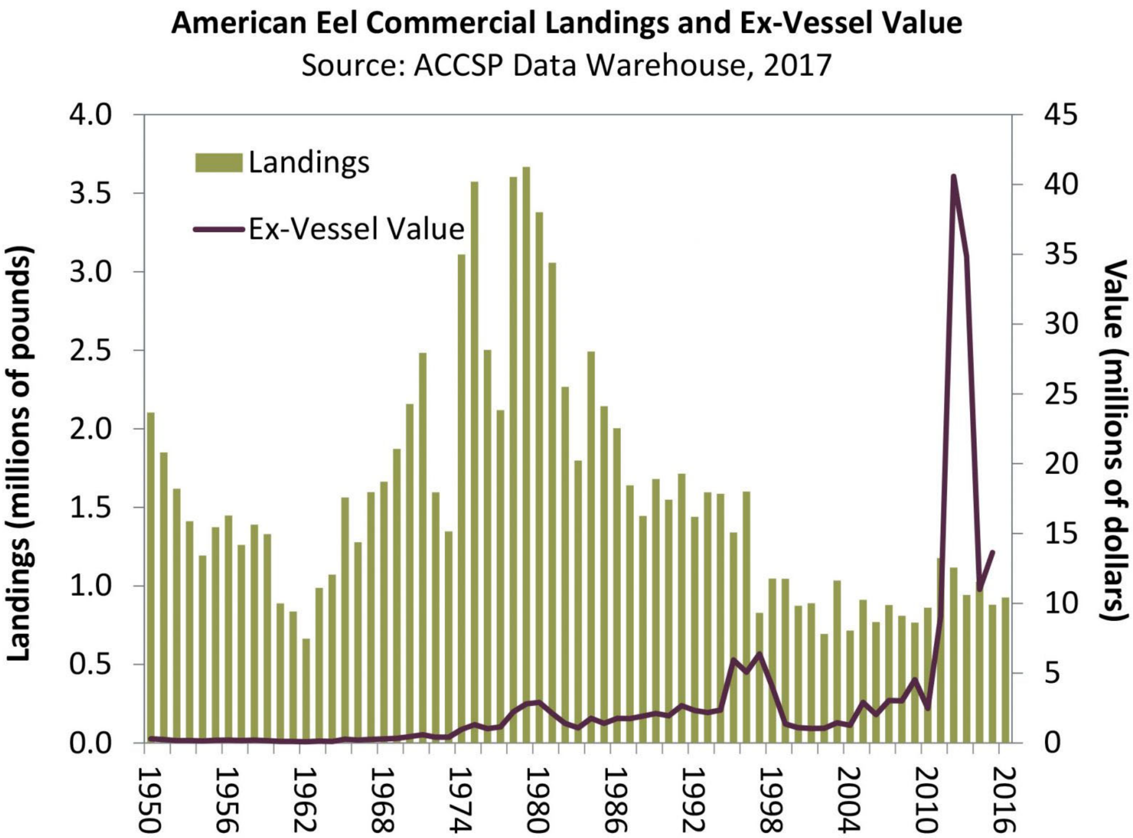

Fig. 2. American Eel (*Anguilla rostrata*) commercial landings and ex-vessel value, 1950-2016. and recreational landings. Fisheries peaked in the late 1970s and 1980s with landings between 2.5 and 3.6 million pounds, but dropped to 1.6 million pounds in 1987 and have remained at lower levels ever since. Graph by Atlantic Coastal Cooperative Statistics Program (ACCSP), retrieved from Atlantic States Marine Fisheries Commission website (ASMFC, 2019). Used with permission.

The average catch size increased after peak fishing occurred, but only because recruitment was so poor. This is most likely attributed to both the high exploitation rates and hydropower dams (Lafontaine et al., 2010).

In the 1970s, adult (silver) eel populations began to decline in the St. Lawrence River Basin, the largest catchment colonized by American Eel (and once the most important fishery in Canada), with cohorts particularly weak since 1988. Eel catch declined from 400 t per year in 1990 to 72 t in 2007 (Management, I. A. C. o. F., 2008) and the species has dropped to <1% of historic levels in this basin (Verreault et al., 2012) although there has been some recovery (Lafontaine et al., 2010). Starting in 1980, total catch declined in both the U.S. and Canada, most likely due to overfishing and dams (Lafontaine et al., 2010; Shepherd, 2006) although (Kahn, 2019) presents an alternate analysis suggesting the fishery has been stable since 2003 and that the continued low abundance is more consistent with loss of access to habitat because of dams.

In some areas, eel abundance remains high. Electrofishing surveys in Penobscot and Kennebec rivers in Maine found eel were sometimes the largest fish biomass, and often the most numerous species, particularly in lower reaches (Yoder et al., 2006). On the Hudson River tributaries, American Eel were the most numerous fish in the tributaries surveyed (Machut et al., 2007).

Exploitation rates (percent mortality with harvest) vary with life stage and fishing gear. Glass eels are harvested only in Maine (with a smaller fishery in South Carolina). A yellow eel fishery still exists in all states except PA and DC. Baited pots are the most common gear, used in rivers, lakes and estuaries. There is a large yellow eel fishery in the Chesapeake Bay, with regulations varying by state but all having at least a 22.5 cm minimum size limit. For further details on these regulations see (Walker et al., 2017) and (Walker et al., 2019).

In 2017, the Maine state legislature authorized the Maine Department of Marine Resources to renew the elver license lottery but capped total licenses at 425." (Resources, M. D. o. M., 2018a). In August 2018 the ASMFC approved Addendum V to the American

Eel Fisheries Management Plan. The Addendum went into effect on January 1 2019. It increases the yellow eel coastwide cap to 916,473 pounds and adjusts the management trigger for reducing total landings when the coastwide cap is exceeded. Maine's glass eel quota is maintained at 9,688 lbs, with an additional 200 lbs of glass eels to be harvested in domestic aquaculture (ASMFC, 2018a, 2018b).

CLIMATE CHANGE

Climate change has been implicated in short-term phenotypic changes of traits in diadromous and marine fish, including age at maturity, age at juvenile migration, growth, survival, fecundity and timing of reproduction (Crozier & Hutchings, 2014). This is significant for species with phenotype plasticity, such as American Eel.

Past climate change events have led to fluctuations in the American Eel population. A historic genetic bottleneck of two orders of magnitude occurred in response to climate cooling during Wisconsinian glaciations, and increased during Holocene (Lecomte-Finiger, 2003; Wirth & Bernatchez, 2003). The medieval warming period also changed Native Americans' methods for capturing eels, with many stone fish weirs built during this time (Peterson, 2018).

Present day climate change can affect American Eel in various ways. On small scales, it can affect river discharge events and therefore migration patterns. It is expected to cause additional droughts, which would cause fewer eels to migrate. On the other hand, it may bring about more extreme weather events, such as hurricanes that are very important for migration, especially for larger eels who tend to migrate during these times (Welsh & Liller, 2013).

Water temperature is a migratory cue for American Eel and it has increased by 0.5 °C over the last century. Eels tend to migrate in warm temperatures and high water levels, with temperature appearing to be the main factor affecting fall (seaward) migration. To test the impact of temperature on American Eel, catch statistics from the St. Lawrence River Basin from 1843 to 1872 were compared to data from 1963 to 1990. Years after 1990 were not included because of sharp population declines. Significant differences in migration time were found between the two periods, with migration always starting at least 10 days earlier during 1963 to 1990. Migrating eels were intercepted on average 18 days earlier although migration ended at about the same time. The resultant longer migration time exposes eels to higher fishing pressure and predation and therefore higher mortality (Verreault et al., 2012).

Climate models predict changes to the gulf stream in response to warming (Shepard, 2015b). The North Atlantic Oscillation (NAO) is correlated with survival and recruitment of American Eel. It may be affecting currents that carry larvae to continental rearing areas by changing ocean productivity that affects larval food availability or by changing the characteristics of ocean front spawning sites south of the Sargasso (Bonhommeau et al., 2008a; Bonhommeau et al., 2008b; Friedland et al., 2007; Miller et al., 2013).

In addition to temperature, eel migration is related to high spring flow. These variables are related as higher winter temperatures indicate the spring flood will probably be lower (i.e., less snow leads to less flow). As the current water level in this basin is about 1 m lower than during the 19th century and the spring flood has been shortened by three weeks, it is expected that American Eel should be migrating later. As they are in fact migrating earlier, the effect of temperature might be even more pronounced in the absence of water regulation. The St. Lawrence River Basin has been profoundly altered by anthropogenic impacts, especially dams and barriers that restrict eels mainly to its lower reaches. The shorter travel distance could provide an alternative explanation for earlier migration, as eels could still be leaving at about the same time but arriving sooner to the estuary (Verreault et al., 2012).

Since dams and warmer temperatures have resulted in lower water levels this should cause later migration, so the fact that eels are still migrating sooner means the effect of warming temperatures may be even more severe than currently realized. The shorter travel distance resulting from barriers may also cause earlier migration. A longer time frame for migration puts eels more at risk of predation (Verreault et al., 2012).

In rivers, abiotic factors such as salinity can affect juvenile eel abundance. Abundance is highest in oligohaline habitats (0.3 to 3.2 ppt), declining in areas with very high or low (<0.1 ppt) salinity. As climate change patterns (such as El Niño events or sea level rise) can affect salinity gradients of estuaries in North America, they can alter freshwater species composition and distribution as well as coastal fish assemblages. By affecting the distribution of juvenile eels, climate change may skew sex ratios as well (Luers et al., 2009).

Climate can affect the entire population by affecting the Sargasso Sea. Climate warming of the Sargasso Sea would inhibit spring thermocline mixing and nutrient circulation, with negative impacts on productivity and therefore food availability for larval eels (Bonhommeau et al., 2008a; Bonhommeau et al., 2008b; Knights, 2003). High temperatures in the Sargasso Sea may be related to gyre spin-up that affects major ocean currents, slows eel larvae migration and increases mortality by starvation and predation (Knights, 2003). In the 1980s, major changes to the ocean current variation in the Sargasso Sea led to the sharp decline of the European Eel (Baltazar-Soares et al., 2014).

Primary productivity of Sargassum has already declined due to harvest (which has now stopped), but rising temperature is shifting the entire Sargasso Sea northward. Warming could also reduce the mixed layer depth where larvae feed and weaken or alter the Gulf Stream, which is necessary for American Eel larvae to migrate (Velez-Espino & Koops, 2010).These factors can increase eel larvae mortality while decreasing recruitment (Bonhommeau et al., 2008b) as well as impact silver eel spawning (Friedland et al., 2007).

SARGASSO SEA

The Sargasso Sea is the world's only habitat comprised of the holopelagic seaweed *Sargassum*, which hosts a rich and diverse community including many endangered and threatened species. The Sargasso is located outside the jurisdiction of any national government and threatened by human activities such as overfishing, pollution, acidification, shipping and Sargassum harvesting (Laffoley et al., 2011). Over the last several decades, increased sea temperatures have lowered primary production and food availability, increasing larvae mortality and lowering eel recruitment (Bonhommeau et al., 2008b) as well as affecting locations of spawning areas by silver eels (Friedland et al., 2007).

One option for conserving the Sargasso Sea is to declare it a marine protected area (MPA) and open ocean refuge for marine wildlife). The Sargasso Sea Alliance (www.sargassoseaalliance.org) has published a plan for doing so called the *Hamilton Declaration* using the existing U.N. Law of the Sea and has received support from several countries. Turning the Sargasso Sea into a MPA could protect both American and European Eels in addition to greatly increasing the amount of protected ocean worldwide (Alliance, 2014).

MPAs have had generally positive effects on biomass, numerical density, species richness and size of organisms within their boundaries. The effects are consistent despite considerable variability in the location (latitude) and size of reserves, although some taxa benefit more than others (Lester et al., 2009). Reserves have been effective at restoring fish biomass and community structure in areas depleted by overfishing (Aburto-Oropeza et al., 2011), although it may take many years for tangible results to be achieved.

While acknowledging the successes of marine protected areas, some authors have expressed doubt that they will be effective at stemming current losses of marine biodiversity because of large gaps in coverage of critical ecological processes related to individual home ranges and dispersal of migratory species, plus practical concerns such as financial constraints, development and difficulty in enforcing protective measures (Mora & Sale, 2011).

AQUACULTURE

Anguillid eels are high-value aquaculture species because of their nutritional properties and acceptance by consumers in East Asia and Europe (Liao et al., 2002). Although it is possible to spawn American Eel in captivity, none of the larvae has survived to adulthood (Oliveira & Hable, 2010). Efforts are further along in Europe (Mordenti et al., 2014) and Japan, although not commercially viable (Tanaka, 2015). If the technical and economic barriers to raising eels entirely in aquaculture were overcome, it could be possible to use captive-bred eels either for food production or restocking efforts. There are some companies that are raising American Eel (such as *American Unagi*, www.americanunagi.com) but thus far all of eels raised in captivity were sourced as juveniles from the wild.

The goal of sustainable aquaculture is to maximize benefits while minimizing impacts on natural and social environment (Frankic & Hershner, 2003). Raising carnivorous fish, however, has the potential to result in net food losses as low-value wild caught marine fish are used as feed fish (Baum et al., 2005; Donaldson, 1997; Naylor et al., 2000; Pauly et al., 2002).

There are a variety of alternate protein sources available for fish feed (not specific just to eels) such as plant protein, including soybean meal, alfalfa leaf concentrate and canola oil, which have been used in aquaculture for catfish and trout (Naylor et al., 2000). Another option is microalgae, which has been shown to be cost effective (Das et al., 2015) and can be more sustainable than other fish feeds (Olsen, 2011; Taelman et al., 2013). Fish feed made from on insect-based protein has wide consumer acceptance in testing (Ankamah-Yeboah et al., 2018; Mancuso et al., 2016) although it does not necessarily result in lower feeding costs (Rehbein, 2013). Oleaginous yeast can also be used in fish feed, as a replacement for vegetable oil (Blomqvist et al., 2018).

Although there has been optimism that alternative protein sources have the potential to improve feed conversion efficiency and reduce excretion of nitrogen and phosphorous (Donaldson, 1997) this does not occur in every case. Diets with fish meal often have better feed conversion ratios than alternative land-based proteins, as has been observed in sea breams (Yone & Fujii, 1975) and cobia (Zhou et al., 2005), because these diets better mimic what fish eat in their natural environments. Land-based protein can also negatively affect nutritional characteristics of farmed fish. For example, in tilapia replacing dietary fish oils with alpha-linolenic acid-rich oils reduced Omega 3 content (Karapanagiotidis et al., 2007) and substituting cod liver oil with corn oil reduced n-3 fatty acids and docosahexaenoic acids (Al-Souti et al., 2012).

Eels raised in aquaculture may be used in restocking efforts. One benefit of this is that in aquaculture, the percentage of glass eels surviving to adulthood is very high (>90 %) (Sara Rademaker, pers. comm. 2019, *American Unagi*), much than in the wild. On the St. Lawrence River, 3.8 million glass eels of American Eel were added between 2005 and 2009. Classes from all four years survived with high growth rates and gonad development plus migration patterns identical to native fish, but long term studies are needed to know if they will successfully spawn (Pratt & Threader, 2011; Verreault et al., 2010). As freshwater eels take longer to reach reproductive age, it is recommended these areas be managed more conservatively. An additional advantage of aquaculture is that it may be possible to lower the incidence of parasites and pathogens using vaccines (Liao et al., 2002) or other treatments such as amoxicillin (Hung et al., 2019) or dietary *Bacillus amyloliquefaciens* (GB-9) and *Yarrowia lipolytica* lipase2 (YLL2), which boost non-specific immune system defense in eels (Zheng et al., 2019). Formalin is also effective against some parasites and commonly used in aquaculture (Leal et al., 2018) and praziquantel has been used to control parasites of the genus *Pseudodactylogyrosis* in Anguillid species (Larrat et al., 2012).

Because American Eel is panmictic with no population structure, restocking efforts could take eels from Canada to the Southeastern United States (or vice versa), a strategy that would not work for species with more complex population structures such as salmon (*Salmo* spp.) or sturgeon (Acipenseridae) (Prosek, 2011). Restocking eels is not a panacea however since stocked individuals can have different growth rates and sex ratios compared to naturally recruiting eels in the same water body (Stacey et al., 2015) in addition to carrying parasites across watersheds (Morrissey & McCarthy, 2008)

POLICIES & LEGISLATION

The status of the American Eel has been the subject of debate in recent years. In May 2004 ASMFC asked USFWS to conduct a Status Review. The ASMFC did not petition to list the species. The USFWS began the process after the request. The Status Review was preempted on November 12, 2004 when Timothy Watts and Douglas Watts filed a petition with the USFWS and NMFS to list the American Eel as an endangered species under the ESA. The Watts petition resulted in the 2007 ESA decision. The Council for Endangered Species Act Reliability (CESAR) petitioned the USFWS to add American Eel to the endangered species list in 2010. The FWS conducted a 90-day finding in 2011, stating this species may require federal protection as a threatened or endangered species (Racey & Miller, 2011). In 2015, the USFWS again declined to place American Eel on the endangered species list, based on their review that found the species remains present across a wide geographic range, the population is considered depleted but stable and some factors (such as fish passage) had improved (Shepard, 2015b).

The ASMFC assessed the American Eel population as "depleted" in 2012 and again in 2017 (ASMFC, 2012, 2017a). In 2014, the IUCN classified American Eel as "endangered" (Jacoby et al., 2017). The IUCN assessment was based primarily on the ASMFC's 2012 stock assessment and the COSEWIC reports (Canada, C. o. t. S. o. E. W. i., 2006, 2012) from Canada.

In Canada, American Eel is considered endangered in the province of Ontario (Ontario, 2018), but not nationally. Under the Species at Risk Act (the Canadian analog to the ESA), American Eel is listed as "no schedule, no status" (Canada, G. o., 2019). The non-regulatory body COSEWIC, the Committee on the Status of Endangered Wildlife in Canada, lists American Eel as threatened (Canada, G. o., 2016). Since the early 1980s, eels have disappeared in the St. Lawrence River headwaters at rates up to 99% (MacGregor et al., 2009; Marcogliese & Casselman, 2009; Verdon et al., 2003).

In 2010, several states petitioned the USFWS to investigate illegal eel poaching under the Lacey Act. In response, USFWS launched Operation Broken Glass from 2010 to 2014 in collaboration with the U.S. Department of Justice's Environmental Crimes Section, the National Oceanic and Atmospheric Administration (NOAA) and numerous state agencies. Poaching was discovered in six states and as of June 2018, 19 eel smugglers had been sentenced (Ebersole, 2018; Walker et al., 2019). The Maine fishery responded to the poaching by implementing a swipe card system to track eel sales in real time for the 2014 fishing season.

The price and supply of Anguillid eels are very complicated issues. The Japanese Eel *A. japonica* is preferred by Asian aquaculture operations, but it has been in decline for decades as a result of overharvesting. The second preference is European Eel, but export of this species was banned in 2011 (Musing et al., 2018). In 2018 however Japanese Eel recruitment plunged again, which drove up the price of American glass eels to record highs of over $6,600/kg in Maine and led to renewed poaching efforts, causing the Maine eel season to close two weeks early (Walker et al., 2019). In November 2018, two men were charged with making illegal cash purchases during the 2018 Maine elver season (Trotter, 2019). American Eel are also harvested in Canada and parts of the Caribbean, but that is beyond the scope of this review.

The 2019 Maine elver season opened on March 22, 2019 with several changes from previous years. Elver dealers can only do business at a single address. Harvesters and dealers are required to completely empty any vehicle-based elver containers – such as aerated live tanks on trucks – when transferring the contents to storage facilities (Rappaport, 2019). Additionally, elver exporters must notify the Maine Marine Patrol 48 hours prior to packing and shipping eels so that an officer from the MMP can weigh, pack and mark the package with a seal that must remain intact until the eels arrive at their destination (Whittle, 2019).

SOCIAL SCIENCE & CULTURE

Historically, one overlooked area in eel conservation is bringing in the human element of how eels have played an important role in many cultures. This has changed in recent years with the publication of James Prosek's book *Eels: An Exploration, from New Zealand to the Sargasso, of the World's Most Mysterious Fish* (Prosek, 2011) and the follow-up documentary *The Mystery of Eels* (Nature & Prosek, 2013).

Citizen science programs can help provide data for researchers in addition to promoting civic engagement and ecological education among the general public. One of the most successful eel science programs is the Hudson River Eel Project, coordinated by the New York State Department of Environmental Conservation Hudson River Estuary Program and the Hudson River National Estuarine Research Reserve, as well as the Water Resources Institute at Cornell University. Since its inception in spring 2008, volunteers have recorded glass eels and environmental data along Hudson River tributaries. From March to May, glass eels are counted, then transported and released above dams (Phillips et al., 2019). As of 2018 it encompasses 14 sites ranging from New York City to Troy and 750 volunteers, with an average of 183 glass eels per day, in addition to environmental data (Conservation, 2019).

Eel education programs are now available in schools as well, such as the *Eels on Wheels* program by Hudson River Sloop Clearwater Inc. This program features live eels and incorporates math, geography and life sciences (Inc., 2019). In 2017, I launched a website and social media group called “Eel Town” (https://www.eeltown.org), named for the historical but unofficial nickname of Brunswick Maryland. The group now includes over 750 members in 25 countries including scientists, fishers, aquaculturists, artists and educators. The town of Brunswick now includes an exhibit at the Heritage Museum on Native American stone fish traps that were used to catch eels, many of which are still visible on Google Earth to this day (Peterson, 2018). Because the eels were so common in this part of the world and a major part of the diets of many Native American tribes (Giles et al., 2016), in a way they represent the biocultural history of the landscape. There is still a great deal to discover about the relationships between humans and eels in this part of the world and how this traditional knowledge can be incorporated with modern science.

CONCLUSIONS

The American Eel faces threats from overfishing, barriers, pollution, climate change, habitat degradation, parasites and changes to the Sargasso Sea. This has resulted in the population becoming depleted, although not necessarily endangered. An integrative conservation management plan combining can help this species recover by considering animal, human and ecological interactions using an approach that combines natural sciences, social sciences and culture. This can include removing dams or adding fish passage provisions, climate change mitigation, advances in aquaculture, restocking efforts, education and outreach programs, citizen science and a change in public perceptions and attitudes.

Long term studies over a wide geographic area could help determine the best management practices for American Eel. Many aspects of the life stages, life history, migration patterns and spawning behavior of American Eel remain unknown. Most studies, particularly on yellow-phase eels, have been done in the Northeastern U.S. and Canada, with few from the mid-Atlantic, southern U.S. or tropical region (Kwak et al., 2019; Welsh & Liller, 2013). A better understanding of the eel population and the factors that affect it can aid fisheries managers and policymakers in creating efficient eel recovery plans.

CHAPTER TWO: AMERICAN EEL (*Anguilla rostrata*): ELVER FISHING IN THE UNITED STATES

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The American Eel historically was the most abundant fish by biomass in North America, found in all watersheds east of the continental divide (Prosek, 2011). Eels are capable of living in more habitats than any species of freshwater fish and may be found in coastal marine waters, estuaries, rivers and lakes (Shepard, 2015b). American Eel leptocephali (larvae) are transported by ocean currents from spawning sites in the Sargasso Sea to the Atlantic coast by ocean currents. Eight to twelve months after spawning, leptocephali begin to metamorphose into glass eels as they approach estuaries and the tidal portions of rivers (Facey et al., 1987). Arrivals occur during winter and spring, beginning in the south and proceeding northward (Helfman & Bozeman, 1984; McCleave, J. D. &

Kleckner, 1982); glass eels can tolerate a wide range of salinity and become pigmented elvers shortly after arrival to coastal waters. Elvers grow into the yellow eel stage (Lecomte-Finiger, 2003), which can last anywhere from 3 (Day et al., 2012) to 25 years or more (Thibault et al., 2007b). Ultimately, yellow eels metamorphose again to become silver eels, before returning to the Sargasso Sea to complete their life cycle. Although never documented in the wild, apparently silver eels die after spawning (Helfman et al., 1987).

Despite considerable research, no one has successfully cultivated eels from egg to maturity in captivity; hence, all American Eels that are harvested and sold, from glass eels to silver eels, are wild caught and have begun life in the Sargasso Sea. Most juvenile eels are sold live to Asian markets, where they will be raised in aquaculture and later resold, sometimes returning to the USA, where eel sushi is becoming increasingly popular (Prosek, 2011). Generally purchased by weight, one pound of glass eels includes 3 000 to 7 000 individuals (Ricker & Squires, 1974) (6 600 15 400 per kg) with the numbers even higher from Caribbean waters (local fishers pers. comm. 2018). Although yellow eels are also harvested in the USA, they are used primarily as bait for commercial and recreational fishing of other species.

Management of the American Eel stocks in the USA is overseen by the Atlantic States Marine Fisheries Commission (ASMFC), which was formed as an interstate compact in 1942 to coordinate the conservation, management and sustainable use of state fisheries resources with representatives from 15 East Coast states (Commission, A. S. M. F., 2018a). In 2000, the ASMFC promulgated the first Fisheries Management Plan (FMP) for American Eel, with the goal being “to conserve and protect the American Eel resource to ensure its continued role in its ecosystems while providing the opportunity for commercial, recreational, scientific, and educational uses" (ASMFC, 2000b).

In 2012 – and again in 2017 – the ASMFC assessed the American Eel stock as depleted (ASMFC, 2012, 2017a). No single cause is responsible, but many contributing factors have been proposed including commercial fishing; habitat loss, pollution, barriers to fish passage, parasitic infections (e.g., the invasive nematode *Anguillicoides crassus*), climate change and changes in the Sargasso Sea (Shepard, 2015b; Walker et al., 2017). On two occasions, in 2007 and 2015, the outcome of petitions for listing the American Eel under the Endangered Species Act (ESA) were deemed not warranted by the U.S. Fish & Wildlife Service (Shepard, 2015b), although both assessments relied on sparse coastwide datasets. The IUCN Red List however does list the American Eel as endangered (Jacoby et al., 2017), as does the Canadian province of Ontario (Ontario, 2018).

Multiple factors have increased international demand for American glass eels in recent years. The European and Japanese species are similar in taste and had previously been preferred for aquaculture. The European Eel has been in decline since the 1970s, with a 90-95% decline in recruitment across wide areas of its geographic range. It has been listed on the IUCN Red List as critically endangered for the past decade (Jacoby & Gollock, 2014). In 2010, the EU banned imports and exports of all stages of European Eel outside its borders (Ebersole, 2017). The Japanese Eel is also in decline and was listed as endangered by Japan's Environment Ministry in 2013 and appeared on the IUCN Red List the following year. The capture of silver eels has been restricted in some parts of Japan since 2012 (Jacoby & Gollock, 2014). It has been reported in the U.S. media that the 2011 tsunami wiped out stocks in Japanese Eel farms and drove up prices of American glass eels, but this is not the case. While the tsunami reduced inland fisheries by about 15% (Craig, 2016), it occurred in the north of Japan, while the glass eel catch and farms are in the south (Pols, 2014).

In the second half of the 20th century, there were glass eel fisheries in the U.S.A. all along the coastal states from Florida to Maine, although never in any of the gulf states (ASMFC, 2000b). Today, Maine has the largest commercial glass eel fishery on the east coast, with a much smaller fishery in South Carolina. Colloquially, "glass eel" and "elver" are often used interchangeably, but these terms are not biologically synonymous. The glass eel stage begins when the leptocephali metamorphose to an eel-like but transparent body morphology, 4.8 to 6.5 cm in length (ASMFC, 2006c). Glass eels are differentiated from elvers, which are pigmented and usually 6.5 to 9.0 cm (Hardy, 1978), ranging up to 15.25 cm in length (ASMFC, 2006a). The variability in size reflects the fact that the term "elver" may include several age classes, with young-of-the-year (YOY) first-year elvers defined as fish less than 8.5 cm. YOY are sampled annually at various sites because this is the one time when it is possible to determine that all of the eels are from the same cohort (ASMFC, 2000a). Another way to tell them apart is that a glass eel will glow bright green under a UV light, while an elver will not (Kumagai et al., 2013).

In the original FMP, the term "yellow eel" refers to eels > 10 cm in length, although this distinction seems variable among coastal states. In 2006, the length was updated to 15.25 cm in a joint meeting of the ASMFC American Eel technical committee and the stock assessment subcommittee (ASMFC, 2006a). In yellow eel fisheries, gear and size restrictions, such as a 0.5 x 0.5" mesh for nets and a minimum size of 22.5 cm in eel pots, are implemented specifically to prevent the harvest of glass eels (Walker et al., 2017).

Randall Livingston, the first recorded commercial eel buyer in the USA. (Ebersole, 2017), entered the glass eel fishery in 1952 (Thomas, 1985). The market took off two decades later in 1972, in response to demand from Japan (ASMFC, 2012), which remained strong until 1977. That year, minimum size limits were imposed in Virginia (15 cm) and Massachusetts (10 cm), effectively ending glass eel fishing in those states ((CBP), 1991). The fishery collapsed the following year due to market conditions (ASMFC, 2000a) and in Maine remained poor until the mid-1990s (Resources, M. D. o. M., 2018a).

Georgia imposed a 15 cm minimum in the early 1980s. From the mid 1980s to early 1990s, glass eel fisheries were established in Connecticut, Rhode Island, New York, New Jersey, Delaware and South Carolina. According to some fishers, there were very few glass eels in 1988, but they returned the following year. The reasons for this resurgence are not clear, but fishers often attribute such fluctuations to natural cycles in eel reproduction and environmental conditions. The Potomac River fishery closed in 1992 when a 15 cm minimum was imposed. From 1992 to 1995, New York, Rhode Island, Delaware, Maryland and North Carolina also instituted 15 cm minimums (ASMFC, 2000a).

The fishery began to grow again in 1994. The following year, the ASMFC convened the American Eel Board to address concerns over the growing exploitation of this species (ASMFC, 2018b). Virginia issued two permits to fish for glass eels for aquaculture in 1996. New Jersey had an active fishery in the mid-1990s but closed in 1998 (ASMFC, 2000a). Maine once had a silver eel fishery, which ran from late summer to fall using weirs across streams and rivers, but it was closed in 2014 (ASMFC, 2013c; Resources, M. D. o. M., 2018a). New York has the only silver eel fishery that continues to this day, with nine permit holders on the Delaware River (ASMFC, 2014).

By the late 1990s, four states had glass eel fisheries – Maine, Connecticut, South Carolina and Florida (ASMFC, 2000a). Some have described the glass eel fishery of the 1990s as an "outlaw fishery" (local fishers, pers. comm., 2018). Regulations varied widely by state and were not well enforced. This was caused by market conditions – although Maine has the most coastline of any state in the conterminous U.S.A., eels arrive sooner to southernmost states because of warmer waters and proximity to the Sargasso Sea.

In 1998, glass eels were selling for US$300/lb (US$660/kg) in Maine. The market declined the following year however, with prices tumbling to US$10-15/lb (US$22-33/kg) and rising only slightly in 2000 to US$25/lb (US$55/kg). As a result of lower prices and the FMP, the Maine fishery was considerably reduced. Gear restrictions went into effect and the duration of the season was shortened, with fishing effort declining by at least 79% (ASMFC, 2002). The only types of gear now authorized for use in Maine are dip nets, fyke nets or Sheldon eel traps (Resources, M. D. o. M., 2018a). As a result of the low prices (approximately US$25/lb, [US$55/kg], for 4 years), hundreds of fishers chose not to renew their licenses. New rules stated that if licenses were inactive for three years, they were automatically revoked. The Connecticut fishery closed around this time as well.

Four American Indian tribes (the Maliseet, the Mi'kmaq, the Passamaquoddy and the Penobscot) are also authorized by the state of Maine to issue fishing licenses because of their ancestral rights under historical treaties. Each of these tribes was once part of the

Wabanaki Confederacy, also written as Wabenaki, Wobanaki or Waponahki, which translates to “People of the First Light” or “Dawnland” (Corporation, 2018). Tribes have the authority to issue licenses, but not to create alternative management plans or other restrictions (Maine DMR, pers. comm. 2018), although the Passamaquoddy tribe has created their own eel management guidelines as part of their tribal fisheries plan (Sipayik, 2013). A discussion of the legislation pertaining to tribal fisheries is beyond the scope of this chapter, but see the Maine Indian Tribal-State Commission for an overview of the relevant statutes, http://www.mitsc.org/library.php?do=section&name=Statutes (Commission, M. I. T.-S., 2018b). There are no tribal fisheries in South Carolina.

The history of tribal fisheries is complex. Native Americans have fished for yellow and silver eels for millennia and eels reportedly were even served at the first Thanksgiving (Prosek, 2011). Historically, the tribes would move throughout the year, often staying closer to the coast in the summer and further inland in winter. During colder months, yellow eels were a reliable source of food. Prior to when Randall Livingston began exploiting glass eels in the 1950s however, there are no records of anyone fishing for them in the U.S.A. Conflicts between tribal and state-licensed fishermen have been reported. Points of contention include differences in licensing systems, quota allocations and territorial disputes over good fishing spots. Tribal fishers have invoked their ancestral heritage and sovereign rights as agreed to in historical treaties, while state fishers have felt their own fishing rights are undervalued in comparison. Official relations between these groups of fishers remain strained and how to resolve the conflicts that arise continues to be a legally contentious issue.

As of 2000, South Carolina had ten permitees (a practice that has continued to this day), although only two were active that year (ASMFC, 2000c). All fishing in South Carolina is restricted to the Cooper River, although at various times in the early 1990s and in 2008 there were experiments with fishing on the Santee River. Many of the details regarding glass eel fishing in South Carolina are confidential under the "rule of three", where any aggregate of data (e.g. month, year, area, gear, quantity landed or quantity sold) consisting of fewer than three fishery identities (of all relevant types) is considered confidential and cannot be shared, because in cases of only two identities someone with the data of one identity could determine the data of the other. This is done to protect the proprietary interests of fishers (Management, O. o. F., 2018).

Florida had no glass eel landings in 2001 or 2003-2005 (numbers were not available for 2002) (ASMFC, 2002, 2004, 2005, 2006b). Florida briefly had a glass eel harvest in 2013-14 but stopped again in 2015 (ASMFC, 2015). South Carolina had no glass eel landings in 2003 or 2004. Glass eel landings in Maine were 14 000 lbs (6 363.64 kg) in 1998 but dropped to a low of 1 282 lbs (582.73 kg) in 2004 (ASMFC, 2006c). In 2004 and 2005, because so many had exited Maine's fishery, the Maine Department of Marine Resources (DMR) held a drawing to give out more licenses. By 2006 prices were still so low that licenses were being given to anyone who requested one, with some leftover.

The FMP was modified in 2006 with the passage of Addendum I, which established a mandatory catch and effort monitoring program with new reporting requirements (ASMFC, 2018b). By that time, all states except Maine, South Carolina and Florida had implemented a minimum size of 15 cm for yellow stage American Eel (which was later changed to 22.5 cm). Glass eel landings continued a general decline throughout the 2000s (ASMFC, 2006c), although reported landings for Maine were 3 735 lbs (1 697.73 kg) in 2007 and 6 051 lbs (2 750.45 kg) in 2008, with an additional 0.1 lbs (0.05 kg) from South Carolina (ASMFC, 2009). In 2008, the American Eel Board approved Addendum II, which included measures to improve eel abundance and recruitment by facilitating the escapement of silver eels during or just prior to their spawning migration (ASMFC, 2008).

In the early 2010s prices increased sharply in response to international demand. By 2011, glass eels were selling for nearly US$900/lb (US$1 980/kg) on average, with landings of 8 548.9 lbs (3 885.86 kg) reported that year in Maine, valued at US$7.7 million. The majority (6 384.48 lbs, 2 902.04 kg) was taken with fyke nets, with the next most common type of gear being dip nets (1 973.64 lbs, 897.11 kg). No gear type was reported for 226.78 lbs (103.08 kg) (ASMFC, 2013a). The following year, glass eel prices were already over US$2 000 per lb (US$4 400/kg) (ASMFC, 2012), with landings in Maine totalling 20 764 lbs (9 438.18 kg) (ASMFC, 2013a). With higher prices however the incentive for poaching increased and in 2013 the ASMFC's law enforcement committee found a significant amount of glass eels being poached outside of South Carolina and Maine (ASMFC, 2013c).

In 2012, the ASMFC's 2012 Benchmark Stock Assessment found the American Eel stock to be depleted. As a result, Addendum III was ratified in 2013, with the goals of reducing mortality and increasing conservation of the American Eel stock across all life stages (ASMFC, 2013c). The Addendum increased the yellow eel size limit from 15 cm to 22.5 cm and reduced recreational creel limits from 50 to 25 eels per day (ASMFC, 2018b).

Until 2013, eels could be bought and sold in Maine for cash, which made it difficult to track buyers and sellers. This meant glass eels were sometimes sold off the books and landings were underreported, with poaching and illegal sale of eels across jurisdictional lines identified as a major problem. In some cases, international eel smugglers have resorted blending multiple eel species together to sell them at the price of the more expensive species. This has happened in different ways, with shipments being intentionally mislabelled, or paperwork changed at border crossings to bring in species like the endangered European Eel. DNA sequencing has the potential to reduce mislabelling in the future.

In response to the higher prices and poaching, Maine switched to a quota-based system for the 2014 fishing season. For the first year, the quota was set at 11 749 lbs (5 340.45 kg) as a 35% reduction from the 2013 harvest of 18 081 lbs (8 218.64 kg). In part because landings were only 9 688 lbs (4 390 kg), the 2014 quota has been retained for subsequent years (ASMFC, 2018b). This statewide quota is divided up among individual license-holders. These “allocations” are based on previous individual catch records, so quantities vary from person to person.

At the same time that the quota system was implemented, Maine began requiring all transactions use a swipe card, with cash no longer accepted to buy and sell eels. This had been requested by many harvesters and dealers. With the swipe card system, all glass eel sales are tracked in real-time. This resulted in a huge decrease in the number of fishery-related infractions reported by the Maine Marine Patrol, from over 200 in 2013 to under 20 between 2014-2016. In 2015, there was only a difference of 120 lbs (2%) between what dealers reported purchasing from harvesters and what was exported from Maine dealers, which was attributed to shrinkage (die-off after initial purchase) and did not raise concerns (ASMFC, 2016, 2018b).

Tribes receive 14% of the total quota, with the Maliseet receiving 106.6 lbs (48.45 kg), the Mi'kmaq 38.8 lbs (17.64 kg), the Passamaquoddy 1,356.3 lbs (616.5 kg) and the Penobscot 620 lbs (281.82 kg) (Resources, S. o. M. D. o. M., 2018b). The Passamaquoddy tribe has a derby-style fishery, which means each member can catch as much as they want up to 10 lbs (4.55 kg) until the entire tribe reaches their quota. The Mi'kmaq have a total of 8 licenses with 4.85 lbs (2.2 kg) for each fisherman. Discrepancies between the quotas and totals reflect a buffer for slight overages.

The quota system also increased the number of tribal fishers. In 2013, there was a dispute over the number of licenses issued by the Passamaquoddy. The tribe was statutorily authorized to issue 200 licenses, but instead issued 575, which put the state over the limit of 744 total licenses established by the ASMFC's FMP. In 2014, when the ASMFC implemented the quota system, the state of Maine worked with the Passamaquoddy to provide them with the authority to issue an unlimited number of licenses through a Memorandum of Agreement, which is renewed annually (Maine DMR, pers. comm. 2018).

Licenses and enforcement work differently in South Carolina. There is no swipe card system, primarily because it would be very expensive to implement such a system with ten or fewer fishers. Fishers are required to report their catches daily; however, these reports are confidential and under the rule of threes the total harvest cannot be published. As such, exact numbers are not available for all years. In 2010 and 2011, the total harvest in South Carolina was under <500 lbs (227.28) each year. In 2012, the total amount is unknown, but was under <5 000 lbs (2 272.73 kg). The highest year on record is 2013, with 2 270 lbs (1031.81 kg). The numbers were lower in 2014 and 2015, with 203 lbs (92.27 kg) and 124 lbs (56.36 kg). In 2016, the latest year for which numbers are available, the total harvest was <500 lbs (227.28).

South Carolina limits fishers to 10 fyke nets per licensee, with dipnets also permitted. Until now, fishers have been limited to the Cooper River, but starting in 2019 nearly all of the rivers in the state will be open. The allowed catch limit will be 700 lbs (318.18 kg), with each of the ten license holders receiving 70 lbs (31.82 kg). This allowed limit keeps South Carolina landings from exceeding the 750 lb trigger that mandates additional life cycle studies. There were ten license holders for the 2018 fishing season. One person can only hold a single license, family members may each hold a license.

Addendum III had also put restrictions on pigmented eels, allowing a maximum of 25 individuals per lb (55/kg) in glass eel landings, using an 8” screen to keep pigmented eels out. This posed some challenges in South Carolina, where many pigmented eels in the Cooper River pass through the 8” screens, causing some fishers to exceed the limit. This caused a number of fishers to leave the fishery, because they had been selling pigmented eels before and now their activities were far less profitable, leading to a reduction in landings from 2013 to 2014. Another reason for the reduction was that South Carolina restricted the fishery in 2014 to in-state residents only, in an effort to reduce poaching (South Carolina DNR, pers. comm., 2018).

In October 2014, the ASMFC approved Addendum IV, which aimed to reduce overall mortality and improve conservation of American Eel primarily through management recommendations for the glass eel fishery. Additionally, any state or jurisdiction with a glass eel fishery had to implement a fishery-independent survey of American Eel covering glass, yellow and silver stage eels within at least one river system (ASMFC, 2015).

Under Addendum IV, states could submit aquaculture plans for harvesting up to 200 lbs (90.9 kg) of glass eels for use in recirculating aquaculture systems (RAS). In 2015, North Carolina submitted a request to the ASMFC for harvesting glass eels for the purpose of raising them in aquaculture. One permit was granted in 2016, but no glass eels were caught due to logistical issues, including delays in the permitting process and fishing late in the season (ASMFC, 2017b).

Addendum V was drafted in October 2017 and has not been finalized at the time of this writing. It proposes new management options, specifically a coastwide cap for yellow eel (with management triggers if the cap is exceeded), as well as potential changes to Maine's glass eel quota and aquaculture (ASMFC, 2017b). Options for glass eel management include the possibility of increasing Maine's quota. In addition, up to 3 states could combine harvest allowances for aquaculture purposes up to a maximum of 600 lbs (272.73 kg) (ASMFC, 2018b).

As prices continued to rise, several states approached the U.S. Fish & Wildlife Service (USFWS) to investigate poaching activity under the Lacey Act, a federal law that prohibits trade in species that have been illegally obtained (Service, 2006). In response, USFWS launched Operation Broken Glass in collaboration with the U.S. Department of Justice's (DOJ) Environmental Crimes Section, the National Oceanic and Atmospheric Administration (NOAA) and numerous state agencies.

The investigation uncovered poaching in North Carolina, South Carolina, Virginia, Maine, New Jersey, Delaware and Massachusetts (Ebersole, 2017). In some cases, dealers sold eels to undercover agents posing as buyers and recording their interactions. As of June 2018, 19 eel smugglers had been sentenced in the U.S.A. (Ebersole, 2018). The cases have been prosecuted in federal district court in Virginia (Justice, 2017a), South Carolina (Justice, 2016b), Maine (Justice, 2016a, 2017c, 2018a), and New Jersey (Justice, 2018b). The Lacey Act carries a maximum sentence of five years and up to U.S. $100 000 in fines, although no one sentenced under Operation Broken Glass has received more than two years (Ebersole, 2018; Justice, 2017b).

In early 2018, Japanese Eel recruitment plunged, with the volume of Japanese glass eels put into aquaculture at only 10% of the previous year (Desk, 2018). This drove demand for American Eel glass eels, with prices surging to record highs of over US$2 800/lb (US$6 160/kg) in March 2018 (Trotter, 2018) (in fact, glass eels were selling for US$3 000/lb, or US$6 600/kg, on opening night, but that was short-lived) and averaging US$2 369/lb (5 211.8/kg) by the end of the season (Resources, S. o. M. D. o. M., 2018b). The sustained demand from East Asia also continued to support illegal exports of European Eels from within the EU (Group & International, 2018).

With prices for American Eel at record highs, several dealers and fishers managed to circumvent the swipe card system during the 2018 fishing season, which led to the DMR closing the season two weeks early. At the time of this writing, the amount of glass eels poached has not been published, but based on the quota total and amount caught prior to the closure, it would have exceeded 500 lbs (227.27 kg). There was a slight overage of 51.66 lbs (23.48 kg) of glass eels by the Passamaquoddy Tribe that will be deducted from next year's total (Resources, S. o. M. D. o. M., 2018b), but this is wholly unrelated to the closure of the fishery.

It is unclear what will happen to the U.S. glass eel fishery in years to come, especially since much of the fishing effort and regulatory response is driven by foreign demand, as well as the supply of other eel species, particularly European and Japanese Eels. As the range of *A. rostrata* encompasses Canada and the Caribbean, it would be helpful in future studies to examine the dynamics of glass eel fisheries in those regions, as well as the effects of yellow and silver eel fisheries on recruitment. Follow-up studies could also include a discussion of additional ways to improve the conservation and management of eels through opening up more habitat by improving upstream and downstream passage, modifying quotas, providing additional options for aquaculture and increasing enforcement measures to reduce poaching.

Acknowledgments

Some of the information in this section was obtained through conversations with commercial fishers, tribal fishers, eel dealers and state agencies. At the request of the publisher and to protect privacy, individual names have not been included. We thank the anonymous fishers and dealers for their contributions.

CHAPTER THREE: DEMOGRAPHICS OF AMERICAN EEL (*Anguilla rostrata*) IN VIRGINIA, MARYLAND AND WASHINGTON D.C.

Abstract

The American Eel (*Anguilla rostrata*) was once very common in the Chesapeake Bay but their numbers have declined in recent decades. The study provides the first overview of the demographics of this species in the states of Maryland, Virginia and the Chesapeake Bay covering several decades of records and in some locations dating from 1911 to 2018. In total, over 3.75 million eels are included in the database. Data collection was inconsistent in many cases, making it difficult to determine trends with regard to sex ratio and levels of infection by the parasitic nematode *Anguillocoloidus crassus* over time. Catch per sampling event (CPSE) shows a decline from 2005 to 2015. Total length data showed males over 40 cm, which is rare in the published literature. I recommend implementing standards for eel collection and data storage and emphasize the importance of open-access data. The primary benefit of this work is the creation of a database of eel abundance and demographics over a large temporal and spatial scale.

Introduction

The American Eel (*Anguilla rostrata*) is a panmictic, facultatively catadromous species (McCleave, J. & Edeline, 2009), with one population that spawns in the Sargasso Sea. Juvenile American Eels are widely distributed by ocean currents from Greenland, Canada, along the eastern United States, to Mexico, the Caribbean archipelago (as far south and east as Trinidad), Central America and South America including portions of Colombia, Venezuela, Guyana, Suriname, French Guiana and Brazil (Benchetrit & McCleave, 2015). This species goes through several life stages and is capable of living in more habitats than any species of fish and may be found in coastal marine waters, estuaries, rivers, lakes and mountain streams (Shepard, 2015b; Tesch, 2003).

Anguillid species are ecologically, behaviorally and sexually adaptive (McCleave, J. D., 2001), exhibiting great variability in growth and tending to be affected by size-dependent biological factors (Shepard, 2015b). Eight to twelve months after spawning, leptocephali (larvae) begin to metamorphose into glass eels as they are transported towards the estuaries and tidal portions of rivers along the east coast of North America (Facey et al., 1987). Arrivals occur during winter and spring, beginning in the south and proceeding northward (Helfman & Bozeman, 1984; McCleave, J. D. & Kleckner, 1982). Glass eels can tolerate a wide range of salinity and become pigmented elvers shortly after arrival to coastal waters. Elvers grow into the yellow eel stage (Lecomte-Finiger, 2003), which can last anywhere from 3 (Day et al., 2012) to 25 years or more (Thibault et al., 2007b). Ultimately, yellow eels metamorphose again to become silver eels, before returning to the Sargasso Sea to complete their life cycle. Although never documented in the wild, silver eels apparently die after spawning (Helfman et al., 1987).

American Eel are intersex before silvering, although sexual differentiation is often complete at 35 cm and eels over 40 cm are traditionally sexed as female (Dolan & Power, 1977) as very few males are found larger than this size (Krueger & Oliveira, 1997). Silvering can begin at three years (primarily for males) to more than 30 years, although six to 416 is typical of eels in the Chesapeake Bay. Females silver at later stages and mean age increases with latitude, i.e., growth is faster in warmer waters (Helfman et al., 1987). Silver eels leave continental waters in late summer and fall to undertake ocean migration to the Sargasso Sea, which is 1,440 km from the Chesapeake Bay (Shepard, 2015b).

The terms "glass eel" and "elver" are sometimes used interchangeably in the literature but the terms are not biologically synonymous. Glass eels are transparent with a body length of 4.8 to 6.5 cm (ASMFC, 2006c), whereas elvers are pigmented and usually 6.5 to 9.0 cm (Hardy, 1978) although they can be up to 15.25 cm in length. This is because "elver" includes several age classes, with young-of-the-year (YOY) first-year elvers being < 8.5 cm in length (ASMFC, 2006c).

The American Eel population has been assessed as depleted. While no single cause is responsible, contributing factors include commercial fishing; habitat loss, pollution, barriers to fish passage, parasitic infections (e.g., the invasive nematode *Anguillicoides crassus*), climate change and changes in the Sargasso Sea. A full discussion of each of these factors is beyond the scope of this article, but see (ASMFC, 2012, 2017a; Shepard, 2015b). The fishery for American Eels consists of both adult eels (coastwide) and glass eels (Maine and South Carolina).

Much of Virginia and Maryland drain into the Chesapeake Bay, the largest estuary in the United States. American Eels are found in more diverse habitats than any other fish because of their adaptability, which allows them to be widely distributed in the tidal and freshwater habitats of the Chesapeake Bay (Jessop, 2010). The Bay ranges from freshwater at the mouth of Susquehanna to nearly full-strength seawater (3.2%) (Fenske et al., 2010). The highest growth rates of American Eel are found in the Choptank River, where 70% are harvested in brackish water. Mean growth rate estimates for Chesapeake Bay eels are generally higher than those in South Carolina, the Hudson River, Rhode Island and Newfoundland (Fenske et al., 2010).

There is no longer a glass eel fishery in the Chesapeake Bay. But there is a large yellow eel fishery, with commercial landings in tidal waters of MD, DE and VA accounting for a large portion of the coastwide harvest (Shepard, 2015b). From the 1950 to 2008, the Chesapeake Bay had the largest harvest (54%) of yellow-stage American Eel in the U.S. (Fenske et al., 2010), with much of that coming from the Potomac River (Fenske et al., 2011). With wide gradients of salinity, depth and temperature this region supports more productive growth habitats for juveniles than other ecosystems playing a key role in the recovery of American Eel as more than 50% of freshwater nontidal habitats have been lost (Fenske et al., 2010). From 1998 to 2013, commercial landings in Virginia waters declined by over 75% from more than 200,000 lbs/year to under 50,000 lbs/year (Shepard, 2015b), although they increased in Maryland from 301,833 to 539,775 lbs (ASMFC, 2014). The results of yellow eel surveys in the Chesapeake Bay have been highly variable. Regional yellow eel abundance indices from 1990-2016 have shown a significant increasing trend (ASMFC, 2017a).

One of the factors affecting eel health is *Anguillicoloides crassus*, a parasitic nematode that infects the swimbladder of Anguillid eels, causing hemorrhagic lesions, fibrosis and swim bladder collapse (Fries et al., 1996). The Japanese Eel *Anguilla japonica* is the traditional host and does not have the same inflammation and pathological changes seen in American Eel (Laetsch et al., 2012) because it co-evolved with *A. crassus* and produces antibodies as a defense mechanism (Knopf & Mahnke, 2004). Infections by *A. crassus* cause physiological damage to the swimbladder, with the extent of the damage proportional to the number of parasites and duration of infestation (Shepard, 2015b).

Buoyancy regulation is not significant for yellow eels who primarily use benthic habitats, but is important for silver eels as they migrate to and locate the spawning grounds, which may occur at depths >600 m (Aarestrup et al., 2009).

The parasite has spread to both Europe and North America, probably due to movement of eels for commercial purposes (Hein et al., 2014) and was first confirmed in North America in 1995 in both Texas and South Carolina (Fries et al., 1996). By the late 1990s, the prevalence of *A. crassus* was 10 to 29% in the Chesapeake Bay (Moser et al., 2001) and it increased during the following decade. Parasite prevalence has been recorded at 42 and 72% in two freshwater (<10 ppt) upper bay locations compared to 18 and 41% at four brackish water (<26 ppt) lower bay locations (Fenske et al., 2010; Fenske et al., 2011). Despite this, there are no significant differences in weight, growth or mortality between infected and uninfected eels in the Chesapeake Bay (Fenske et al., 2010).

Management considerations for the American Eel are limited by a lack of reliable data (ASMFC, 2012)**.** To augment traditional data sources, I compiled a database comprised of landing records of eels in the Chesapeake Bay region over the past century (1911 to 2018) and built a map using ESRI ArcGIS 10.6. The primary objective of this work was to build the largest dataset of American Eel landings over a large temporal and spatial scale, which has never been done in this region, with a goal of providing a basis for future conservation management decisions.

Materials & Methods

Eel data were gathered from several sources: the Virginia Department of Game and Inland Fisheries (including the JFISH collection and data originally collected by the Smithsonian Institution), Maryland Department of Natural Resources (including the Maryland Biology Stream Survey, MDCHES database and SASSFish Index), the U.S. Forest Service Southern Research Station and the U.S. Fish & Wildlife Service. These data were acquired through requests and non-disclosure agreements and cannot be redistributed in raw form, but anyone who wishes to acquire these data can do so by contacting the respective state and federal agencies. The study area is comprised of Virginia, Maryland and Washington, D.C. and covers 1911 to 2018.

The dataset includes over 70 variables, related to both the eels themselves and environmental conditions (Table 1). These include the number of eels caught, the location, date and year of capture, total length, sex, catch per unit effort, presence of absence of *A. crassus*, fishing net mesh dimensions, in addition to environmental data such as water temperature, air temperature, gear, % moon illumination, salinity, pH, pollutants, conductivity and turbidity. In some cases, variables like “site name” and “stream name” were used to determine the location. Eels were captured at all life stages, including glass eel and elver surveys from 2000 to 2009. These data are sparse and not consistent from one collection to the next, so they are difficult to use in the aggregate.

Table 1. Variables in the American Eel (*Anguilla rostrata*) dataset

Time and place	Eel data	Environmental data	Env. Data (cont'd).
Date	Count	Water temp (ºC)	Epifaunal substrate
Site name	# mLs caught	Air temp (ºC)	Velocity/depth diversity
Stream name	Elver/ml used for year	Discharge	Extent of pool/glide (m)
Basin	Max eels/day	Moon illumination/Lunar phase	Riffle/run quality
Latitude	Life stage	Salinity	Extent of riffle/run (m)
Longitude	Total eels	pH	Channel alteration
Hydrologic Unit Code	Sex	Water level	Lab conductance (µmho/cm)
Time sampled	CPUE	Average thalweg depth (cm)	Acid neutralizing capacity (µeq/L)
	Pass 1	Average width (m)	Dissolved organic carbon mg/L)
	Pass 2	Average velocity (m/s)	Chloride (mg/L)
	Eels/hour	Instream habitat structure	Sulfate (mg/L)
	Eels/m^{2-1}	Bank stability	Total nitrogen (mg/L)
	Length	Length sampled	Total phosphorus (mg/L)
	Weight	Area sampled	Ammonia (mg/L)
	Gear	Pool/glide/eddy quality	
	Gear rating		
	Mesh		
	Parasites		

I created a map of the eel locations using ESRI ArcGIS 10.6. The locations were listed in various formats in each dataset, many of which were incompatible with one another. When GPS coordinates were listed, they were used. ArcGIS uses the decimal degree format, so any locations listed in degrees-minutes-seconds were converted using a VisualBasic Macro in Microsoft Excel. The data from Virginia was listed in the form of meters relative to the data frame rather than coordinates. These were converted by first changing the projection in ArcGIS to GCS_WGS_1984 and then using Calculate Geometry tool. About 0.1% (986/772,364) of the Virginia data was stored as polylines or shapes (rather than points) and these were omitted.

For some sites, only a description was given, e.g. “KNIGHT IS UPSTRM-100 M E MILL CK”. I interpreted this to mean “Upstream from Knight’s Island and 100 m east of Mill Creek”. I searched for these locations on Google Earth and Google Maps, plotted the coordinates as best I could, then used the measuring tool in Google Earth to draw a line (in this case, 100 m east of Mill Creek), plotted another point and used those coordinates as the sampling site. In most cases there were other clues I could use to determine if I were in the correct area; for example, this particular site was also listed as being within the Sassafras River basin. Some site names were listed as being in between two locations, for example “LLOYDS CREEK TO KNIGHT ISLAND”. For these, I plotted the locations (in this case, Lloyds Creek and Knight Island) on Google Earth and then measured the midpoint between them. Because of the number of samples with these same descriptions over several dates, I believe these were probably taken along sections of rivers and creeks, with researchers sampling at multiple sites. While the midpoint may not be exactly where the samples were taken, I feel this is an acceptable compromise because the eels could have swam anywhere within that stretch. Over 1,000 locations (each of which could represent many eels) had to be manually verified using this method.

Dates were listed in a variety of formats in the original datasets and were corrected using formulas in Excel. In cases where individual eels had identical dates and collection sites and no other information to differentiate them, these data were combined into single rows with a count for the total number of eels. Over 7,000 rows were eliminated using this methodology.

Where data were available, I attempted to include variables in addition to the date and coordinates. Many of the sampling points included multiple eels and when this was listed, these numbers were included in the counts. A value of “1” was considered the minimum, even though some of the columns listed “0” eels or had blank values. These were nevertheless counted because based on the other columns it often appeared that fish had in fact been caught, with records indicating live eels had been re-released or including additional biological data. Values of “999” were interpreted as either null values and discarded or changed to “1” when other biological information (e.g. life stage) were available. Counts were graphed using Microsoft Excel 2019.

In some cases, life stage was listed in the datasets. In cases when it was not, I attempted to interpret it based on total length. Eels < 15 cm total length were considered glass eels/elvers. I did not attempt to differentiate elvers from glass eels because of the ambiguity of these terms in the literature. Some eels were described as “pigs”, which I interpreted to mean “pigmented elvers” (because they become pigmented as a result of feeding). Eels with a total length ≥ 15 cm total length were considered yellow eels. Because eels spend the vast majority of their lives in the yellow form and only silver just before the downstream migration for spawning, silver eels tend to be rarer in sampling. As such, all silver eels I included were identified as silvering by the collectors.

Sex data were available for some records. I also considered any eel ≥50 cm TL as female, which is a very conservative estimate based on the literature. Eels with a total length <50 cm but no sex were listed as unsexed. Sex data were graphed using the software Past 3.25.

Catch per unit effort (CPUE) was available for only a small number (47) of records. Thus, I created my own estimate, called catch per sampling event (CPSE) by excluding the glass/elver eel counts (which typically number in the hundreds or thousands, because the eels are much smaller during this life stage, in addition to any single eel count ≥100, which may have been unlabeled glass eels), totaling the number of eels in a given year and dividing by the number of samples for that year. These were further divided by state boundaries to determine CPSE for Virginia and Maryland. CPSE was calculated from 1977 to 2018 in Virginia and from 1994 to 1997 and 1999 to 2015 in Maryland. Years were excluded when there were no data or when the data were sparse over time, e.g. one year with data followed by several years without.

All other data were taken verbatim from the original datasets. Presence/absence of *A. crassus* was noted only when the original collectors recorded this information. A graph of the percentage of eels infected by year was made in Microsoft Excel 2019. Water temperature data were provided by the original field collectors. Some data were excluded from analyses when the date or location could not be determined. This removed 1,611 eels from the database. In other cases, environmental data were removed when the numbers appeared impossible, for example water temperature data with a value of 0° C were excluded because I thought it was unlikely any eels were caught when the water was at freezing point. Finally, the data were added to ArcGIS 10.6 as X/Y data. A flowchart of the methodology is shown (Fig. 3).

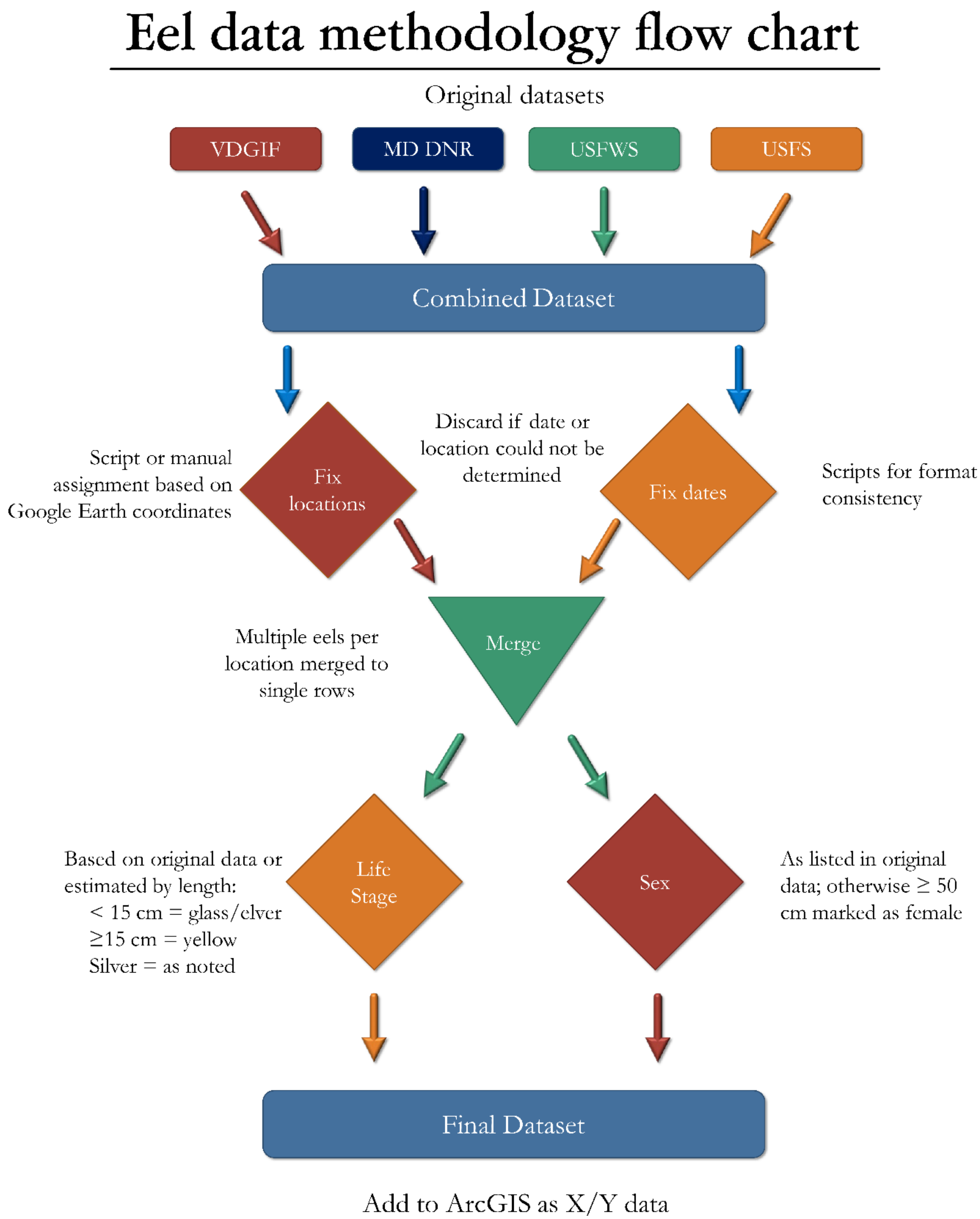

Fig. 3. Flow chart of the methodology for combining the American Eel (*Anguilla rostrata*) datasets. The process started with several original datasets, which were combined into a spreadsheet. Various techniques were used to determine locations, dates, sexes and life stages. The resulting dataset was added to a map with the software ESRI ArcGIS 10.6.

Results

The database contains 21,912 entries, each of which accounts for 1 to 10,000+ eels, representing 3,753,877 eels (Fig. 4).

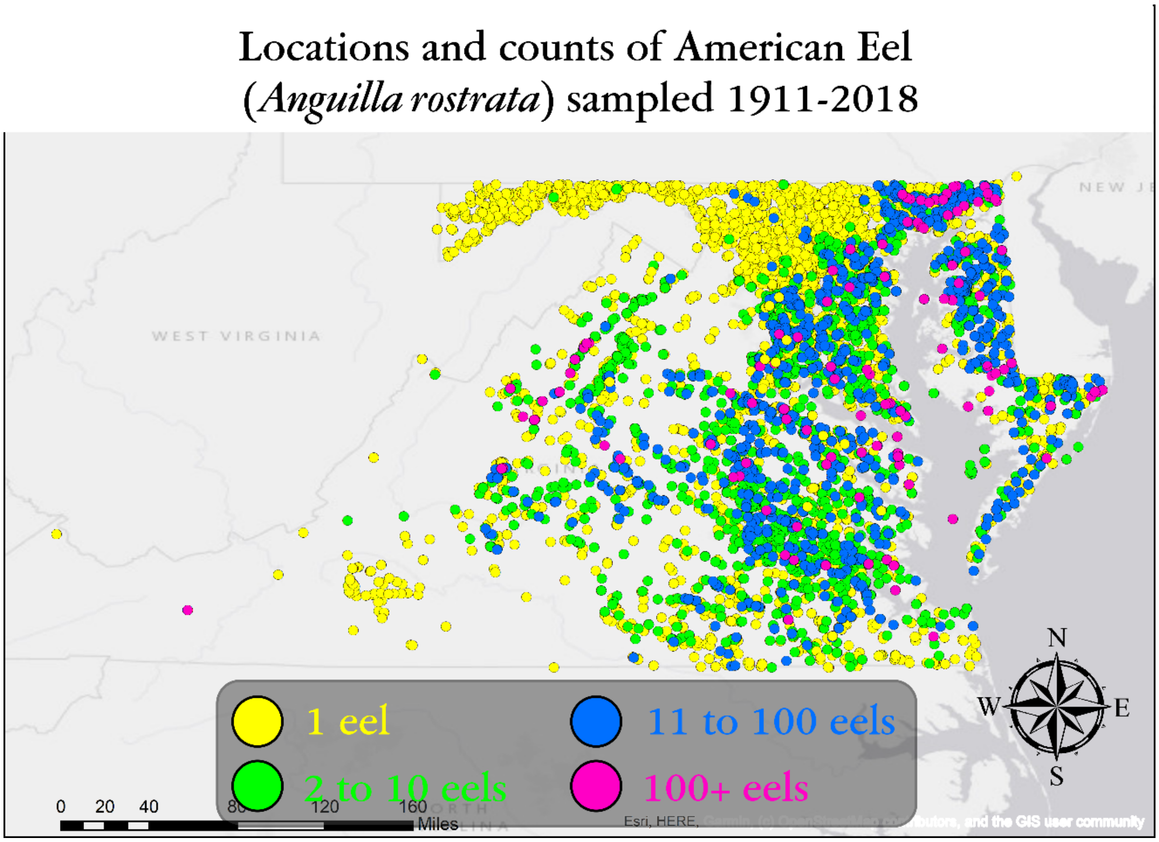

Fig. 4. Locations and counts of American Eels (*Anguilla rostrata*) sampled between 1911 and 2018 in Virginia, Maryland and Washington, D.C. Yellow dots represent individual eels, green dots 2-10 eels, blue 11-100 and magenta >100.

In Virginia, eel collection records date back to 1911, the earliest of which was collected by the Smithsonian Institution. For D.C. and Maryland, records start in the 1970s. Most (3,715,467 or 98.98%) of the eels were collected between 2000-2018, with only 38,410 (1.02%) between 1911 and 1999 (Fig. 5).

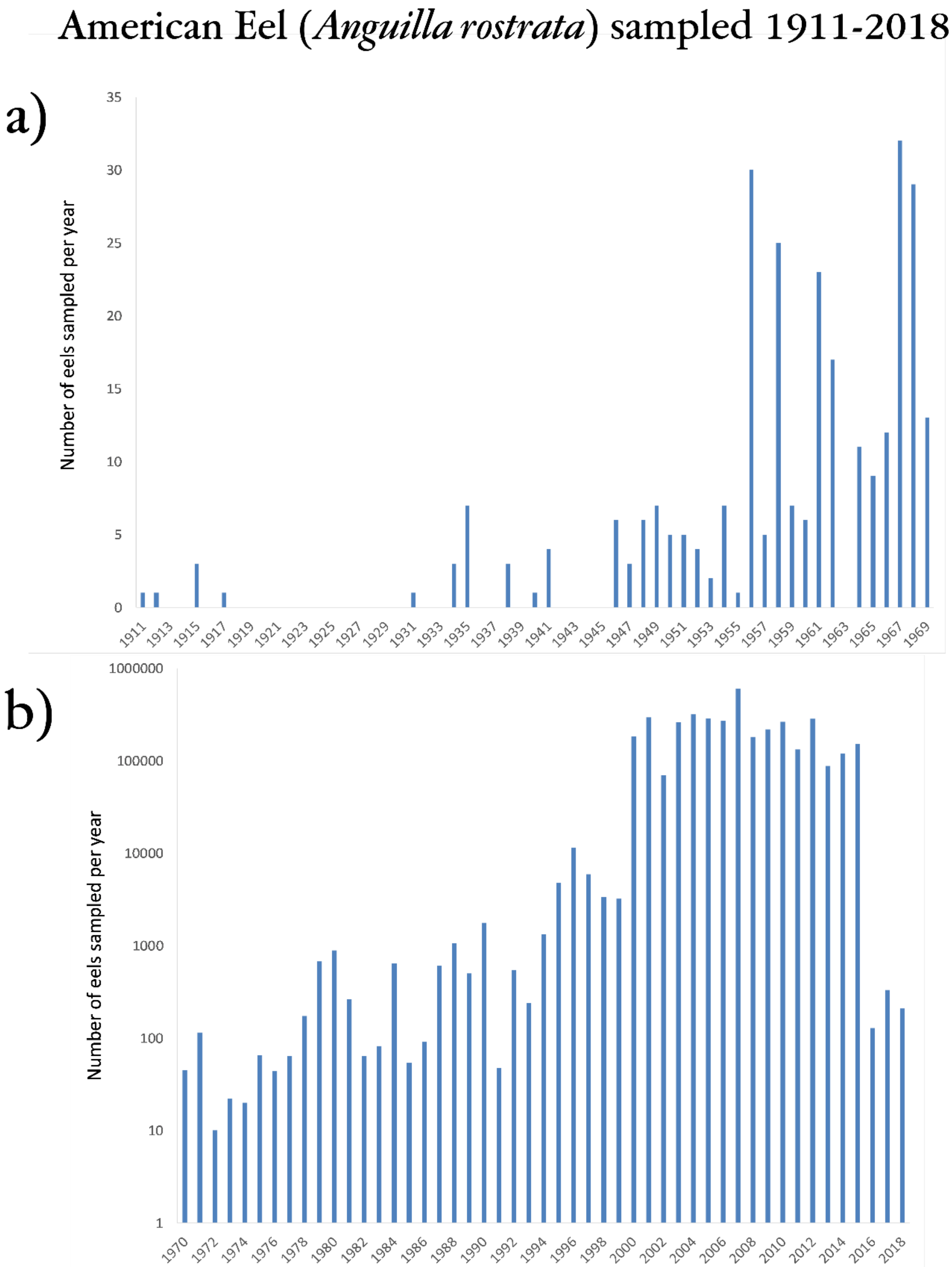

Fig. 5. Number of American Eel (*Anguilla rostrata*) sampled per year from 1911 to 2018. 5a shows 1911 to 1969, while 5b shows 1970 to 2018. Note that before 1970 there were never more than 32 eels caught in one year, whereas in recent years (post-2000) the numbers are frequently in the tens of thousands.

Gear differed among the datasets. Collection methods included backpack electrofishing (14 records), boat electrofishing (309 records), eel pots (5,696 records), a hoop net (one record) and Irish eel ramps (16 records). All other records (15,877) did not include the type of gear used. In some cases, a 0.5x0.5” mesh, 2x2” wire mesh or 0.33x0.33” panel was used to allow smaller eels to pass through. Some of the eel posts are listed as being placed “below the study area”, thus the listed coordinates reflect the river segment but not necessarily the exact location. Some of the pots were listed as containing “fresh razors”, which I interpret to mean razor clams of the genus *Siliqua*. In some cases, the eel pots also caught other fish species, including brown bullhead *Ameiurus nebulosus*, yellow perch *Perca flavescens*, channel catfish *Ictalurus punctatus* and pumpkinseed *Lepomis gibbosus*, in addition to blue crabs *Callinectes sapidus*.

Life stage data were available or could be determined for 2.95 million eels (Fig. 6). The vast majority (>90%) were glass eels or elvers, followed by yellow eels and silver eels. Exact counts are difficult to determine because at some sampling points the eels were classified as a mix of life stages, with yellow and silver frequently grouped together, possibly when the fish were silvering. All glass eels and elvers were found between 2000 and 2009, during June and July. The earliest date was June 22nd (in 2000) and the latest was July 1st (in 2009). Yellow eel data were by far the most common and were available from 1994 to 2018. While yellow eels are present year-round, life stage data on yellow eels were not available for January, February, March or August. Silver eel data was available from 2006 to 2015, with silver eels found from September to December only. The earliest calendar date for silver eels was October 19th (in 2007) and the latest was December 13th (in 2008).

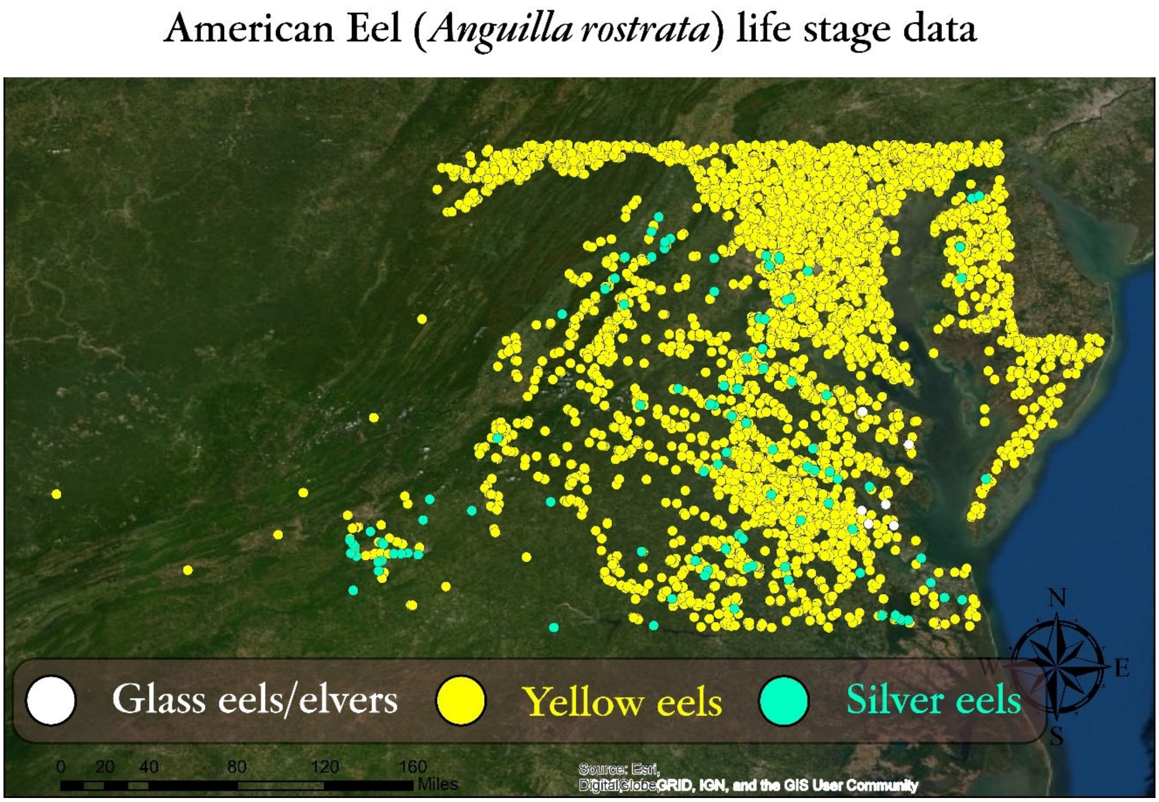

Fig. 6. Life stages of American Eel (*Anguilla rostrata*) sampled in Virginia, Maryland and Washington D.C. White circles represent glass eels and elvers. Yellow circles represent yellow eels. Teal circles represent silver eels. Note that life stage data were not available for all eels sampled.

Weight and total length were available for some eels, all in the yellow stage. Weight data was available for 8,293 eels in the Sassafras and Elk Rivers and ranged from 11.00 g to 1.71 kg, with an average of 74.86 g and a median of 54.00 g. Total length was available for 8,361 eels, from the Sassafras and Elk Rivers as well as from the upper reaches of the Rappahannock and Potomac Rivers. Total length ranged from 15.80 cm to 85.50 cm, with an average of 33.07 cm and a median of 31.20 cm. Eels over 70.00 cm were found only in the Sassafras River, which is a relatively short tributary (35 km) flowing directly into the Chesapeake Bay.

Sex data were available for 5,214 eels between 2000 and 2015, all captured between April and July. The distribution of confirmed male and female eels is shown (Fig. 7). There were 329 males and 394 females identified in the original datasets, in addition to 13 sampling locations with a mix of both sexes comprising the other 4,491 fish. Including all eels $\geq$ 50 cm as female increased the total number of females to 515 with a minimum length of 29.40 and a maximum length of 85.50 cm, a mean of 50.05 cm and median of 51.90 cm. Total length of 310 males ranged from 24.90 cm to 46.80 cm, with an average of 31.22 cm and median of 31.20 cm (Fig. 8).

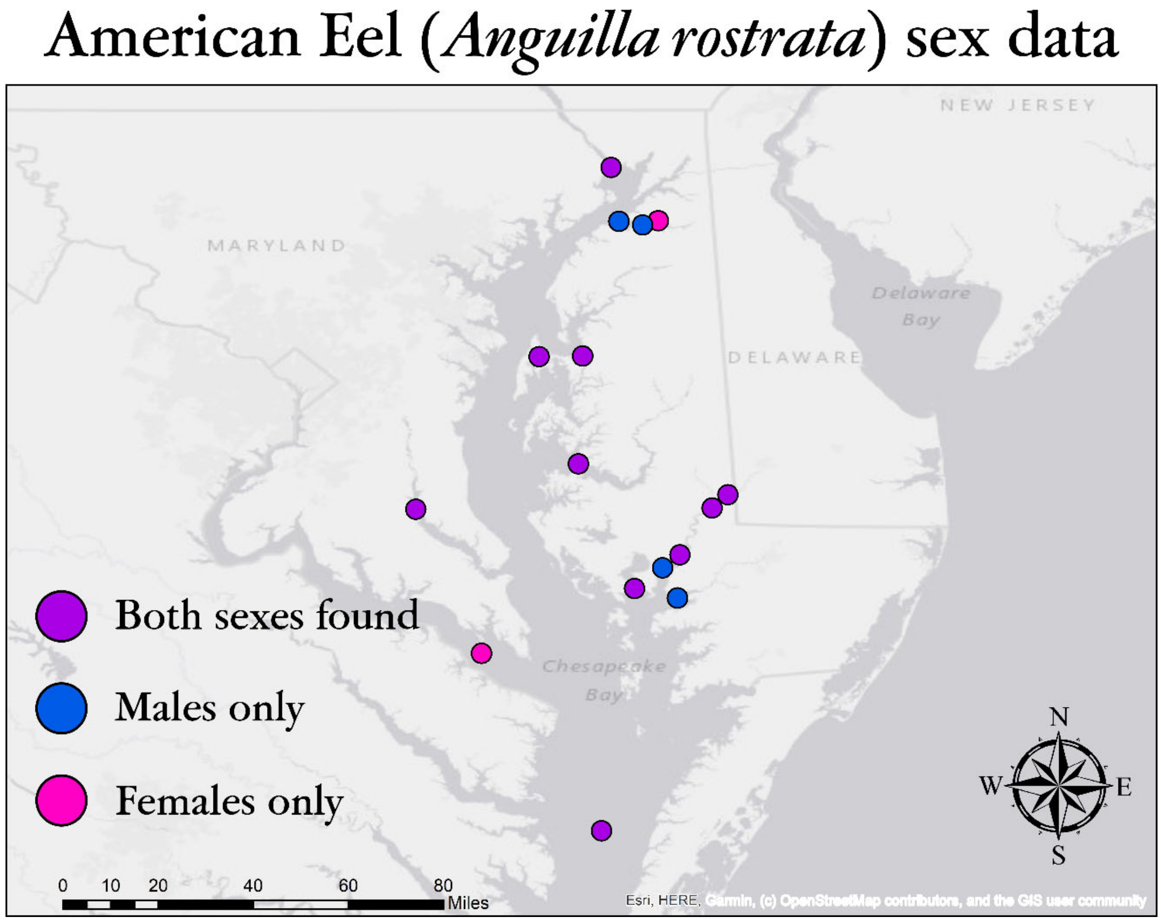

Fig. 7. Distribution of male and female American Eel (*Anguilla rostrata*) in Virginia and Maryland. Blue dots indicate males, pink dots indicate females, purple dots indicate the presence of both sexes.

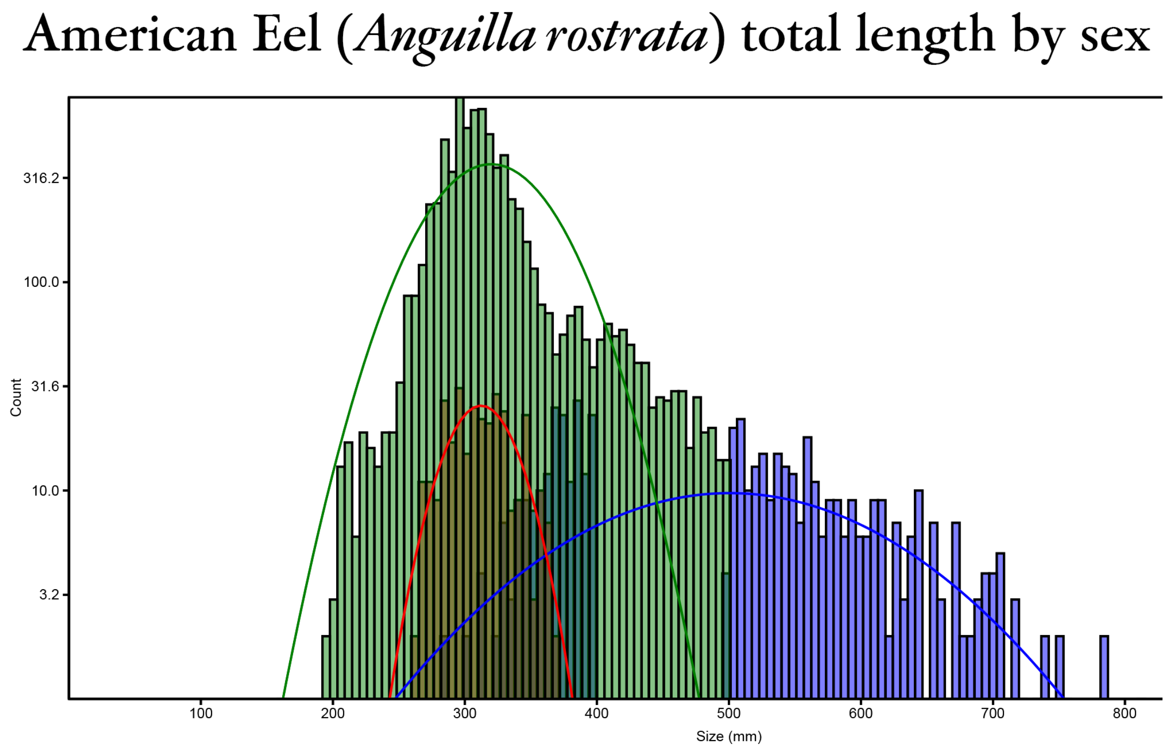

Fig. 8. Graph of the total lengths of American Eel (*Anguilla rostrata*) in Virginia, Maryland and Washington, D.C. as categorized by sex. Males are shown in red, females in blue and sexually undifferentiated eels in green.

Of 244,176 eels caught between 1994 and 2015, 57,486 (23.5%) were parasitized by *A. crassus*, while 186,690 (76.5%) were not (Fig. 9). Numbers varied by year, with a high of 87.43% in 1996 and a low of 0.14% in 2012 (Fig. 10).

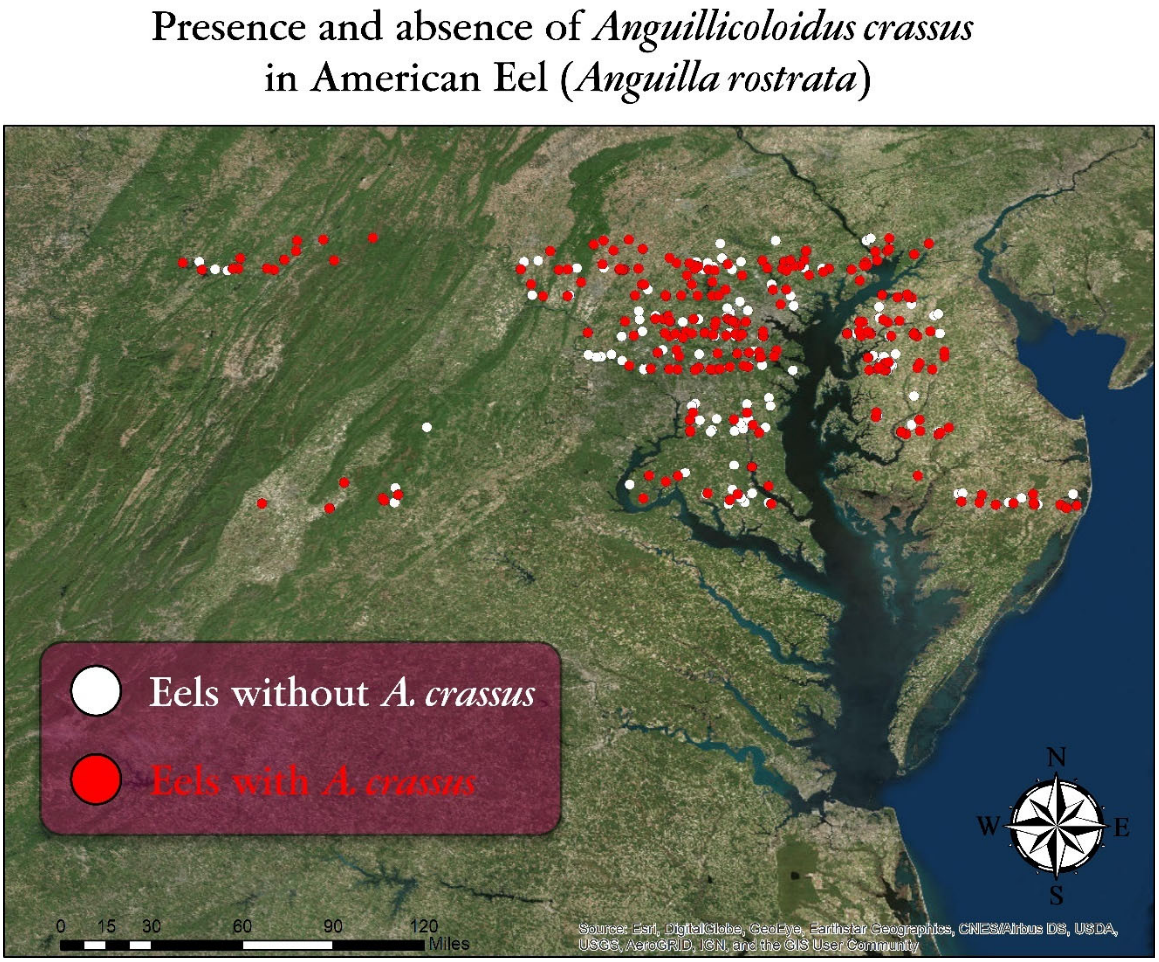

Fig. 9. Presence and absence of *Anguillocoloidus crassus* in American Eel (*Anguilla rostrata*) in Virginia, Maryland and Washington, D.C. White circles show eels free of parasites, red circles show eels with this parasite. Although there are more white circles than red, there were more than three times as many eels without this parasite (76.5%), because each circle can represent many eels.

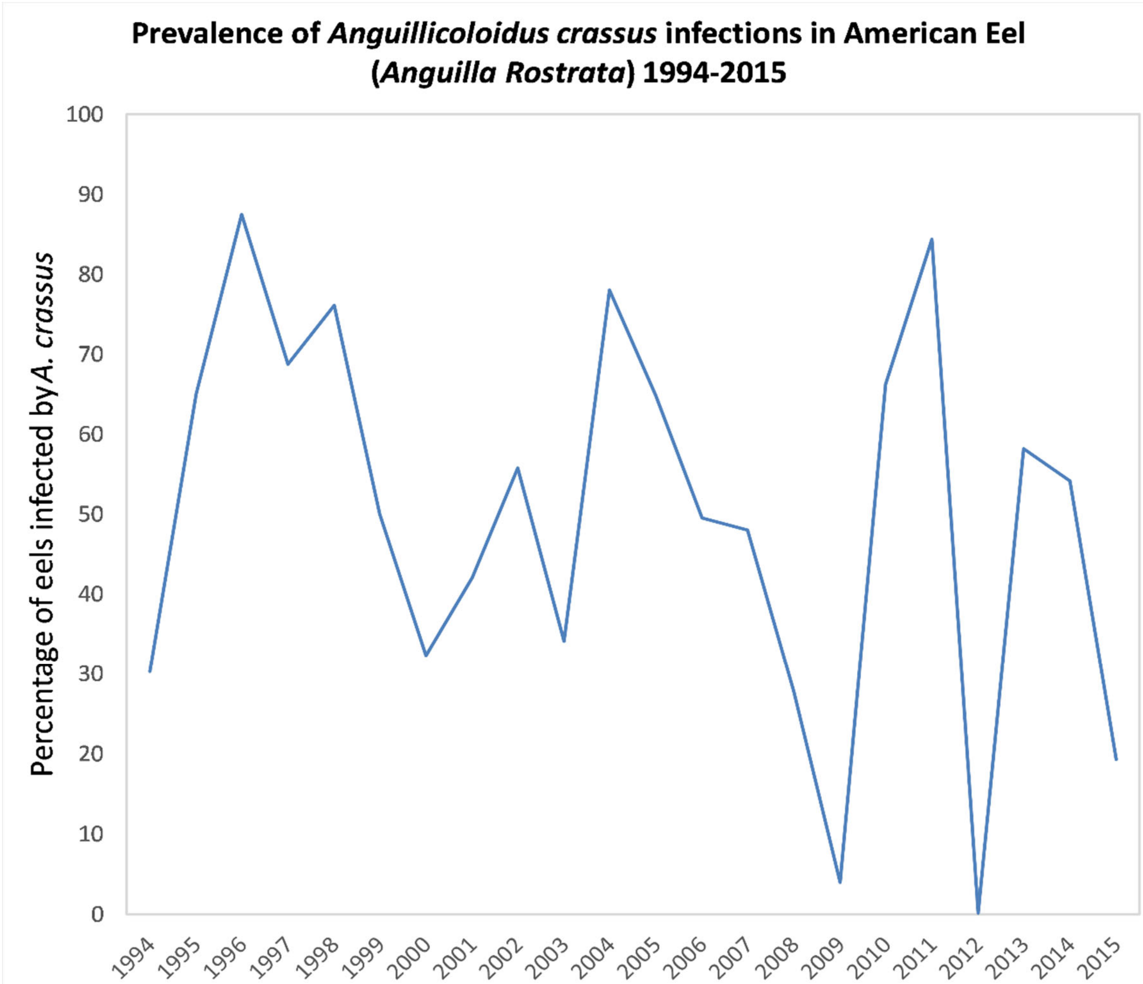

Fig. 10. Percentage of sampled American Eel (*Anguilla rostrata*) infected with *Anguillocoloidus crassus* from 1994 to 2015.

Water temperature data were available for 9,336 sample points (corresponding to 1,908,116 eels). The minimum temperature was 1.5 and the maximum was 30.2 °C. The mean was 24.08 and the median was 25.00 °C.

CPSE varied from year to year, although it declined from 2005 to 2014 (Fig 11).

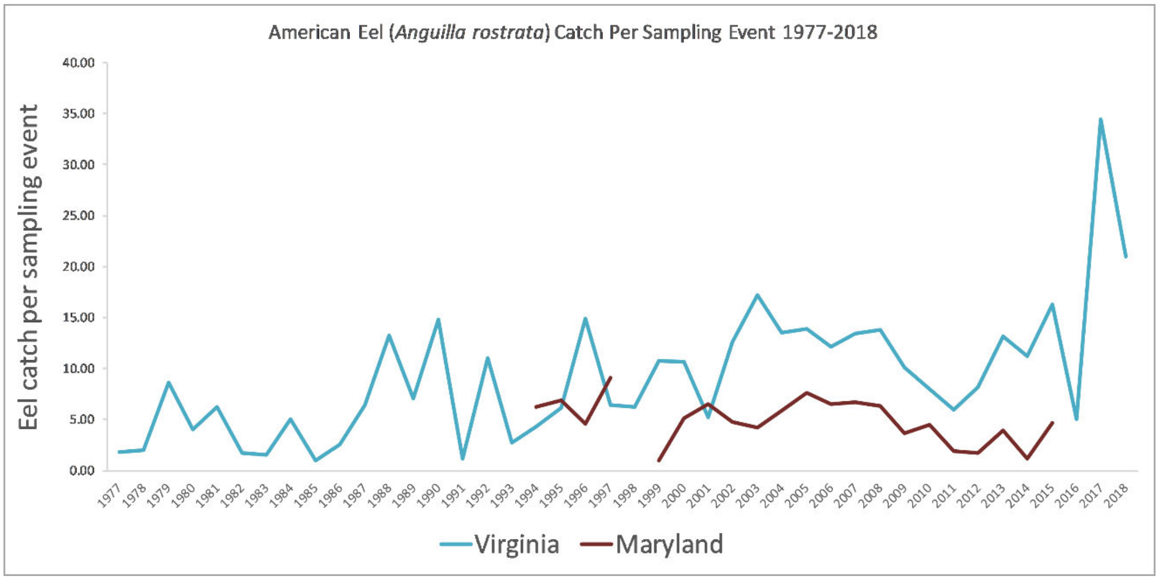

Fig. 11. Catch per sampling event (CPSE) from 1977 to 2015. Values derived by dividing the total number of eels (excluding glass eels and elvers) by the number of samples per year. Data from Virginia run from 1977 to 2018. Although a higher overall number of eels were caught in Maryland these data were more sporadic over time, thus only 1994-1997 and 1999-2015 are included.

Discussion

Based on the map (Fig. 4), eels have been sampled in every major river of the Chesapeake Bay and in many of the smaller tributaries as well. The dataset includes slightly over 3.75 million eels sampled. This is most likely a very conservative estimate, because many of the samples did not include the counts and thus were counted as “1”. The graph in Fig. 5b shows an increase in eel counts in recent years, albeit with a decrease from 2015-2018. This is because data from 2016-2018 were only available from Virginia and these years lack the counts from Maryland and Washington D.C.

Most of the records are from 2000-present. The data are skewed toward recent years, partly because of increased sampling efforts, as noted by the number of entries in the database, with over 75% being from 2000-2018. This can partially be attributed to the glass eel surveys that routinely net thousands of fish, because the eels are much smaller and in higher density during this life stage. CPSE however decreased over a ten year period (2005 to 2014), which is consistent with the ASMFC's findings that the stock has become depleted (ASMFC, 2012, 2017a). The ASMFC does not consider CPUE as being indicative of trends of the stock as a whole because CPUE is generally composed of positive trips only and differences in baiting practices vary geographically, which can impact the accuracy of this measurement (ASMFC, 2017a). This is also likely the case with our own estimate of CPSE. The paucity of data before the year 2000 limits the ability to study the eel population prior to the onset of commercial fishing, 1952 (Thomas, 1985) or the start of the decline two decades later (Jacoby et al., 2017).

It is likely the actual number of yellow eels within the dataset is also likely much higher, since many of the data points in inland areas (the habitat for yellow eels) did not include life stage or total length. The months and days when elvers were captured increase year by year, but it is unclear if this reflects local environmental changes or different sampling times by researchers. The data show silver eels from September to December, which is consistent with most eels although previous studies have documented downstream migration in the Potomac and Shenandoah rivers in every month except July (Welsh & Aldinger, 2014). This may indicate sampling pressure is more common during the fall than other times of the year.

There did not appear to be any clear geographic trend regarding the distribution of males and females, with both distributed throughout the Bay. The sex ratio in the Potomac River becomes increasingly female with distance upstream (Goodwin & Angermeier, 2003), but most of the data on sex distribution were near the mouth of the bay and likely included silver(ing) eels on their downstream migration.

The total length for the larger males (46.8 cm) was surprising because it is widely accepted that female eels are on average significantly larger than males (Krueger & Oliveira, 1999) and that nearly all American Eel over 40 cm in length are female (Dolan & Power, 1977; Krueger & Oliveira, 1997). These results may be explained by the fact that the vast majority (94%) of eels with available total length data were not sexed. A bimodal size-distribution has been documented for silver eels (Davey & Jellyman, 2005), which was confirmed in the data (Fig. 8) but only because I decided to list the larger eels as female. It is not clear why no eels over 40 cm were identified as female by the original collectors. Sex is linked to density (high densities mean more males, lower densities mean more females) (Davey & Jellyman, 2005) but I were unable to determine whether this is supported by the data because there are so few locations with only males or females. Female eels have a bimodal size distribution, with some growing much larger to carry more eggs, at the expense of a longer lifecycle. The larger females can be identified prior to silvering because of their size, but for smaller yellow eels it is impossible to make this determination. This is also problematic for determining life stage, because many of the larger eels may have been ready to silver, although they were listed as either “yellow stage” or “unknown life stage” in the original datasets.

The longest eels were found in the Sassafras River, which is a relatively short (22 mi) tributary leading into the bay. This corroborates previous research, which found eels with a primarily estuarine residence had higher growth rates and total length at migration than eels that reside primarily in freshwater (Jessop et al., 2004). This basin may be a priority for conservation, since the longest eels carry the most eggs.

Eels in saline water tend to have faster growth regardless of sex (Cairns et al., 2009; Fenske et al., 2011) But the Sassafras River is at the top of the bay, where eels typically have lower growth rates (Fenske et al., 2010). In this case the results may again be due to a lack of consistent data. The vast majority of eels did not have any recorded total length and those that did tended to be concentrated in a few areas on the map.

Based on the data, the average number of eels infected with *A. crassus* was 23.5%, which is within albeit near the lower bound in previous studies, which have also shown that the presence of this parasite has increased with time in the Chesapeake Bay (Fenske et al., 2010; Moser et al., 2001). I was not able to confirm this trend however and the variability appears to be due to the inherent inaccuracy of combining multiple datasets, e.g. different locations, different methods, many samples not recording parasite presence/absence. There was no clear geographic trend either, although published research has shown abundance decreases with latitude (Hein et al., 2014).

The results for water temperature data corroborate previous studies, which found that in the Chesapeake Bay eels were found from to 31 °C, with the highest percentage were found from 26 to 28 °C (Geer, 2003). Temperature is also highly dependent on the time of year and time of day of sampling, which may reflect observer bias rather than eel preferences.

This study is the first of its kind to examine demographic data of American Eel over such a large temporal and spatial extent. For future works, this can be expanded further, to include the entire Chesapeake Bay watershed as well as other drainages as the dataset already includes eels from the Roanoke and Monongahela Rivers. One of the biggest challenges however has been resolving the inconsistencies in data recording from each site and collecting agency. Consistent protocols and data storage have the potential to provide much more information and make it easier to analyze. This is one area where something as simple as an "eel data collection app" for smartphones could streamline efforts and greatly aid future researchers.

Traditional collection efforts could also be supplemented with environmental DNA (eDNA) sampling could be an option. In 2019, the first study was published using eDNA to estimate distribution, abundance and biomass of Japanese Eel (*Anguilla japonica*) (Itakura et al., 2019). These authors point out that eDNA can be used to monitor eel populations over large spatial and temporal scales at reduced cost compared to conventional techniques. There are limitations, however: eDNA cannot provide information on individual fish, such as sex, total length, weight, presence or absence of parasites, etc. and the amounts only weakly correlate to abundance. Determining abundance is difficult with commercial landings too, since these also reflect changes in regulations, market prices, consumer preferences and decisions by fisheries managers (Shepard, 2015b). So, fisheries-independent sampling with nets or electrofishing will remain necessary to establish demographics of the population.

Follow-up studies can also add additional layers to the ArcGIS map. For example, *A. crassus* abundance could be overlaid with layers for water temperature, salinity and riparian land use, to see if any trends become evident. Higher salinity and colder temperatures reduce the success of this parasite (Fenske et al., 2010; Shepard, 2015b), although its abundance may increase from anthropogenic impacts, as infection rates are correlated with urbanized land and higher water temperatures (Machut & Limburg, 2008). Since silvering is tied to lunar cycles and lunar discharge (Welsh et al., 2015), lunar phase could be generated from the collection dates and overlaid with silver eel data and salinity to observe the timing of the silvering process over a large geographic range.

The primary benefit of this project is the creation of a database of eel abundance and demographics over large spatial and temporal scales. This opens the door for additional studies using these data, including mapping trends by watershed in ArcGIS or comparing the eel data to dams and land use. But one downside to this study is that, per the non-disclosure agreements required to compile the eel demographic data, these data cannot be shared with the public or other researchers. In my opinion, this is a major detriment to conservation management of data-deficient species like the American Eel.

In conclusion, this study combines the largest database on American Eel demographics, covering Virginia, Maryland and D.C. over several decades (over a century in Virginia). Total length data yielded males over 40 cm, which is rare in the published literature. Sex data was too inconsistent to determine any spatial pattern. The average level of *A. crassus* infection was consistent with previous works although I did not observe any temporal trend. CPSE decreased in recent years although this could be attributed to differences in gear selection and a lack of negative results. I recommend implementing standards for eel collection, such as recording the location in decimal degrees, the total length, weight, life stage, sex when applicable presence/absence of parasites, CPUE or

CPSE and gear used, in addition to environmental data such as water temperature, salinity, pH and pollutants. Some of the records included this information but it was sparse and difficult to draw conclusions from the limited data. Making these data open access will also make it easier for future researchers to build upon the collection data.

CHAPTER FOUR: SPATIAL ANALYSIS OF AMERICAN EEL (*Anguilla rostrata*), FISH PASSAGE AND LAND USE IN CHESAPEAKE BAY TRIBUTARIES

Abstract

Catadromous eels are found in more habitats than any other fish and are capable of inhabiting marine, brackish and freshwater environments. In this study I use American Eel (*Anguilla rostrata*) as a bioindicator organism to create a novel method of using spatial analysis to study species conservation over landscape scales. I built a model of the subwatersheds of the Chesapeake Bay using a Digital Elevation Model (DEM) and overlaid eel density data (> 1 million eels sampled), dam density data and land use in ArcGIS. Dam construction in the study area peaked between 1955 and 1975, possibly as a result of flood control measures. Effects of land use were localized and most pronounced in areas around Baltimore MD, Washington D.C. and Richmond VA. Results indicate the Potomac and Rappahannock rivers appear to be areas of lesser concern while the upper James and York rivers are ideal for follow-up studies, since these area rank poorly in both eel density and barriers to fish passage. Because these rivers have high eel density downstream, the dams appear to be the limiting factor. Sampling methods have been inconsistent over time, making it is difficult to determine where eel densities are low vs. the area having had little sampling effort. This is partially resolved with catch per sampling event (CPSE), which appears to show a relationship between eels sampled and the number caught per sample. Discussion includes potential strategies for improving fish passage.

Introduction

The American Eel is a catadromous species that spawns in the Sargasso Sea and is distributed by ocean currents from Greenland to North and Central America, the Caribbean and northern drainages of South America (Benchetrit & McCleave, 2015). This species can use one of several life strategies and live in saltwater, brackish estuarine water and freshwater (Jessop, 2010; Tesch, 2003). Catadromous eels are found in more diverse habitats than any other fish because of their adaptability (McCleave, J. D., 2001), which makes them ideal candidates for studies over a large geographic region. Eels have been used as bioindicator species for studying environmental contamination in streams (Belpaire & Goemans, 2007) as well as in classroom studies combining biology and geography (Inc., 2019) and citizen science projects (Phillips et al., 2019).

This species goes through a complex lifecycle with several life stages. Larvae drift toward the Atlantic Coast via the Gulf Stream, becoming glass eels upon reaching coastal waters (Lecomte-Finiger, 2003) and pigmented elvers shortly thereafter. Elvers grow into the glass eel stage, which comprises the majority of the eel lifecycle, before going through a second metamorphosis to silver stage and migrating back downstream. Silver eels appear to die after spawning (Shepard, 2015b).

The population has been assessed as depleted in recent years (ASMFC, 2012, 2017a) although the decline was primarily during the latter half of the 20th century and has leveled off in the last couple of decades (Kahn, 2019). Stressors include climate changes, changes in the North Atlantic currents (as well as potentially in the Sargasso Sea), parasites, especially *Anguillocoloides crassus*, habitat loss, pollution, overfishing and barriers (Shepard, 2015b). One of the challenges for American Eel is to be able to migrate upstream into non-tidal habitats (during the yellow phase) and then back downstream during the silver phase. Estuarine habitats used by American Eels have been lost because of filling and conversion to upland, as well as eutrophication and contaminants. Nationally, annual rates of estuarine habitat loss are estimated at 0.9%, averaging 2,240 ha per year (Dahl, 2006). By the late 1990s, an estimated 84% of the freshwater habitat accessible to American Eel had been lost (Shepard, 2015b).

American Eel are able to climb very well for fish and can even travel up Great Falls on the Potomac River (as evidenced by their presence in upstream tributaries, including the Shenandoah River). But some natural and anthropogenic barriers are impassable. Dams may be complete barriers or may restrict eels of certain sizes, or may block eels only during specific flow conditions (Shepard, 2015b). On the Hudson River, eel density upstream of natural and artificial barriers was reduced by a factor of 10, with less biomass as well (Machut et al., 2007) (Schmidt et al., 2009). Eel abundance increased in headwater tributaries following the removal of the Embry Dam in 2004 on the Rappahannock River (Hitt et al., 2012). In other cases, upstream passage facilities are installed, typically sloped ramps with pegs or a rough substrate (Shepard, 2015b). Upstream mobility is particularly important for American Eel because the lacustrine habitats found in lakes, reservoirs and wetlands tend to produce large, highly fecund, female eels, particularly at northern extremes of the range (Castonguay et al., 1994; Shepard, 2015b). Dams can affect eel migration patterns, connectivity and timing (Verreault et al., 2012), restrict the range where eels can live (Hitt et al., 2012), reduce indigenous aquatic fauna and alter riparian vegetation through inundation, flow alterations and influences on groundwater and the water table (Gregory et al., 2002).

For downstream migration, a variety of methods exist to help silver eels safely migrate past dams including trap and transport programs and fish screens to divert eels toward bypass chutes (Eyler et al., 2016). Downstream passage facilities such as weirs and flumes have been used to mitigate effects of turbine mortality, with eels tending to prefer bottom opening bypass weirs (Shepard, 2015b). In a study on the Magaguadavic River in

New Brunswick, only 32% of eels passed safely, with the others entering the turbines and dying (Carr & Whoriskey, 2008). Hydroelectric dams can also delay migration and cause mortality, which can cause silver eels to revert to the yellow eel stage if they encounter obstacles or delays (Winter et al., 2007). Turbines can decrease local and regional abundance and could skew population toward smaller and younger females, and more males (Shepard, 2015b). Downstream migration remains dangerous as eels take the path of least resistance, essentially going with the flow and can be sucked into turbines of hydroelectric dams (Verreault et al., 2012).

Of eels that went downstream through five dams on the Shenandoah River, 2/3 used the spillway and the other 1/3 went through the turbines, with pass via spill over more common during times of high river discharge. Turbine mortality ranged from 15.8% to 40.7% at individual dams. Turbine shutdowns on the Shenandoah River reduced silver eel mortality. A shutdown from 1800–0600 hours protected 81% of downstream-migrating eels. Fifty percent of downstream passage events occurred between September 15 to December 15. There is variability in the migration time and additional dates of turbine shutdowns could protect more migrating eels. There is no investment for these methods although they do carry a loss in revenue (Eyler et al., 2016).

Concerns over eel passage and access to habitat may be compared with salmon on the Columbia River, which is is one of the largest rivers in North America and has been a focal point for fish passage research (Kareiva & Carranza, 2017). Historically, it provided feeding, rearing, and migration habitat for some of the largest runs of Pacific salmon *Oncorhynchus* spp. in the world (Sol et al., 2019), with the Snake River (its largest tributary) once having the most productive salmon habitats in the Northwest (Kareiva & Carranza, 2017).

But for nearly a century the Columbia River has been modified for hydropower, flood control, transportation and irrigation (Ferguson et al., 2007), with 172 large dams today (Kareiva & Carranza, 2017). In addition to the dams, small barriers such as culverts can also negatively impact fish passage. Both dams and culverts restrict access to spawning and rearing habitat, in addition to modifying instream habitats (Sheer & Steel, 2006).

In the latter half of the 20th century, efforts were made to develop screening systems to divert juvenile salmon from turbines during their downstream migration (Williams, 2008). Many improvements were made in fish passage and fish transport during this time and today a large number of salmon survive the journey from their spawning sites to the mouth of the Columbia (Kareiva & Carranza, 2017). Thus, it appears dam removal may not be necessary to save salmon, but there is also the possibility of dams causing delayed or indirect mortality (Kareiva & Carranza, 2017). For example, predatory fishes and birds target juvenile salmon at the base of dams. To remedy this, exclusion devices have been placed at the fishway openings on the Bonneville dam and management agencies have implemented nonlethal programs to deter pinnipeds (McLaughlin et al., 2012).

A second complication is that designs that appear to work well for Pacific salmon (*Oncorhynchus*) on the Columbia River do not always work in other parts of the world (Kemp, 2016) or with other fish species. Thus, when building fish passage facilities to maximize biodiversity, the behaviors and swimming abilities of all fishes must be considered (Noonan et al., 2012). One difference with catadromous versus anadromous fishes is that the salmon swim downstream when they are juveniles, whereas the eels are large adults during their downstream migration for spawning, which may put eels more at risk of turbines (Skalski et al., 2010). Thus, while the lessons from the Columbia River Basin are useful, American Eel conservation may require novel methodology.

Throughout the freshwater habitats used by American Eel, rivers and streams are lined with varying degrees of riparian buffers and urbanized, impervious surfaces. Riparian buffers include both forest and grass buffers, along with shrubs and other vegetation. These are managed to maintain the integrity of stream banks, reduce the impacts of terrestrial pollution and to supply food and thermal protection to fish and other wildlife (Okay & Weammert, 2009). Riparian buffers can shade riverbeds, sustain allochthonous inputs (both of which reduce algal growth), intercept and absorb nutrients, and support diverse habitats for fish communities. Buffers can also provide inputs of leaf litter and terrestrial invertebrates, which provide food for aquatic fauna (Canning, 2018). Urbanization can affect shading, allochthonous inputs, hydrology, water chemistry (by altering stream geomorphology) water quality and invertebrate prey densities (Machut et al., 2007). The relationship between eels and land use is complicated and cannot be taken as simply a causation between more land use buffers and increased eel densities.

To the best of my knowledge no study has examined the effects of land use buffers on American Eel in the Chesapeake Bay watershed, although it has been studied in the Hudson River estuary in New York. In this watershed, American Eel abundance and biomass respond strongly to barriers and secondarily to local-scale urbanization in tributary subcatchments. In some instances, urbanization can result in higher eel abundance, but at a certain point urbanization has negative effects because of the increases in pollution and eutrophication and these authors found significant decreases as urbanization replaces riparian buffers and no eels at all at sites with 30-40% urbanization (Machut 2007). Land use can also affect parasite incidence. Infection rates of Eustrongylides and *A. crassus* in the Hudson River increased with urbanized land, as well as higher water temperatures (Machut & Limburg, 2008). In the Hudson River estuary, eels of all sizes use lifter as cover during autumn and substrate cover during summer. As such, protecting riparian forest buffers can help provide deciduous leaf cover for eels in autumn (Johnson, J. H. & Nack, 2013).

The effect of riparian buffers on eels has also been studied in New Zealand, on both longfin eels (*A. dieffenbachii*) and shortfin eels (*A. australis*). The abundance of both species is associated with increased riparian cover (Glova et al., 1998). There are differences in habitat selection between the two species, but this would not appear to be a factor in North America since there is only one eel species here. In New Zealand, eel total length is associated with riparian habitats. In a short-term case study in New Zealand, removal of overhanging vegetation and in-stream wood from short reaches of a small pastoral stream with intact riparian margins resulted in the formation of shallow uniform runs rather than the pool and riffle structures found in unmodified reaches. This reduced the abundance of adult longfin eel (*A. dieffenbachii*) although elvers became more abundant (Jowett et al., 2009). If these results apply to the Chesapeake Bay, the loss of upstream riparian buffers could result in reduced yellow eel abundance, since elvers are only found at the mouth of the bay.

In some studies however eel presence has been negatively correlated with native New Zealand forests, with greater eel biomass and a density along pastoral sites (Broad et al., 2001). Perhaps paradoxically, eel abundance and biomass are correlated with non-native willow trees (Glova 1994). Eels are largest in areas with pasture, medium in areas with willows and smallest along tussock (grasslands) (Jowett et al., 2009).

The objective of this project was to create a model of eel migration and habitat suitability over a large geographic area by combining biological data on eels with environmental data and a Digital Elevation Model (DEM) of the watershed. Digital Elevation Models have been used in spatial analysis to construct drainage paths for decades (O'Callaghan & Mark, 1984; Tribe, 1992) and my goal was to create an "eel's eye view" of the Chesapeake Bay for migratory eels. This paper is the first to combine over a century of eel abundance and density data across two dozen Chesapeake Bay tributaries along with dams and land use to determine habitat suitability and priority areas for conservation measures. The goal was to create a new model for species conservation using spatial analysis.

Materials & Methods

Using ESRI ArcGIS 10.6.1, I created a map of the Chesapeake Bay to analyze several factors: eel density (and catch per sampling event, or CPSE), presence of dams (with and without fish passage) and land use around streams. The eel data comes from a database I compiled using datasets from the Virginia Department of Game and Inland Fisheries (including the JFISH collection and data originally collected by the Smithsonian

Institution), Maryland Department of Natural Resources (including the Maryland Biology Stream Survey, MDCHES database and SASSFish Index), the U.S. Forest Service Southern Research Station and the U.S. Fish & Wildlife Service.

The compiled database includes variables such as time and location of collection, number of eels, length, weight, life stage and presence/absence of parasites, in addition to CPSE from 1977 to 2015. But these data are sparse and not consistent across collections, years or geographic areas. For example, the type of fishing gear used was only available in about 1/4 of the records and varied between backpack electrofishing, boat electrofishing, eel pots and Irish eel ramps. These were acquired through requests and non-disclosure agreements and cannot be redistributed in raw form. The study area is comprised of Virginia, Maryland and Washington, D.C. CPSE across the entire data set shows a decline from 2005 to 2014, but eel data were analyzed as density (total per km) instead, because CPSE (like catch per unit effort, CPUE) can differ by baiting practices and is biased toward positive trips. The eel counts at least document places where eels have been found, and since the majority (>98%) of the data were from 2000-2018, they should reflect current more than historical densities. The paucity of data before the year 2000 limits the ability to study the eel population prior to the onset of commercial fishing, 1952 (Thomas, 1985) or the start of the decline two decades later (Jacoby et al., 2017).

The database of dams was taken from The Nature Conservancy (Conservancy, 2019). There are 3,828 dams in the Chesapeake Bay watershed. Erik Martin at The Nature Conservancy provided additional data on dams (including which ones have fish passage provisions) (pers. comm.). Land use data for the year 2015 was provided by the Université Catholique de Louvain (Louvain, 2018).

Delineating locations as "land" and "water" required a multi-step process. First, using the ArcGIS tool *Buffer* (Analysis) a 100 km circle was drawn around all eel sample points, with dissolve type set to "All". The "Water Courses – Global Map" shapefile from the USGS was clipped to this buffer using *Clip* (Analysis) and the resulting attribute table was exported to Microsoft Excel format. I created a spreadsheet and traced each segment back to the mainstem of the rivers flowing into the Bay. This made it apparent that some of the eels sampled (approximately 15%) had not come through the Chesapeake Bay, but through other drainages, primarily the Roanoke and Monongahela Rivers. These were excluded from analysis.

To determine the extent of the rivers, I combined four data sources. The first two were from the USGS National Map: Small Scale (https://nationalmap.gov/small_scale/atlasftp.html) (Survey, 2018). I used "Streams, One Million-Scale" and "Water Courses – Global Map", both at 1:1,000,000 scale (100 m). Additionally, I created a map of streams using 20 tiles from the ASTER Global Digital Elevation Model (DEM) dataset with a resolution of 1-arc-second (30x30xm) (Survey, 2014). I used the following Spatial Analyst tools in ArcGIS to generate all streams > 25 km^2: Fill, Flow Direction and Flow Accumulation, followed by the Raster Calculator with *SetNull("bay_flowac" < 27778,1)* to set the minimum threshold to 25 km^2 $(25*10^6)/(30^2)$, then Stream Link, Stream Order and Stream to Feature. The two USGS stream files were merged with each other but could not be merged with the streams I generated from the

DEM, because of differences in the data formats in the attribute tables. So, a 1 km buffer (referring to the *Buffer* (Analysis) tool in ArcGIS, not a riparian or land use buffer) was drawn around the USGS streams and a separate 1 km ArcGIS *Buffer* was drawn around the DEM-created streams (using the Dissolve (All) feature in both cases) and the resulting polygons were merged. The areas marked as water on the land use raster were converted to a shapefile and a 1 km ArcGIS *Buffer* was applied. This was merged with the preceding polygons and another 1 km ArcGIS *Buffer* was used to remove a few gaps and to make the streams more visible when the map is zoomed out. Thus, there is approximately a 2 km polygon around each polyline marked as water. The ArcGIS *Buffers* are necessary because a polyline is a vector with no width and does not reflect the width of streams and creeks in real life.

The ASTER data was used to generate the watersheds as well, using the following Spatial Analyst tools: Fill, Flow Direction, Basin and Raster to Vector. This generated a map with over 300,000 polygons. Polygons that coincided with the river segments were merged using the ArcGIS editor, all other polygons were removed and the remaining polygons were joined to remove the grid created by the initial 20 raster tiles. The resulting polygons each represent watersheds and are hereafter referred to as the study area. Watersheds were further divided into subwatersheds at approximately 50 km along the mainstem. Any watershed with less than 50 km on the mainstem was not subdivided. These subwatersheds were used to calculate the densities of eels and dams and bin the results into categories for ranking.

The generated watersheds do not include the full extent of several rivers for two reasons: 1) the tasks become exponentially more computationally difficult with increased area, especially at high resolution; and 2) I wanted to focus my efforts on the areas where I had eel data, which are Virginia, Maryland and Washington D.C. I removed sections of Delaware, Pennsylvania and West Virginia when mapping the watersheds and do not include the excess areas when calculating eel and dam densities. I believe this is not a significant limitation to this study because the areas closest to the mouths of the rivers are most important for studying the habitats and passage of a migratory species. The state boundaries were clipped after the watersheds had already been generated based on DEM and so some sections (most notably Potomac River 05) are split in half by the boundaries, but the two fragments are processed together in the model because they are still part of the same subwatershed section.

When the eel data were placed on the basemap, it became apparent that much of it did not align with conventional maps of streams of creeks, with eels appearing to be on land rather than water. This may be due to errors in data collection, or eels that were caught from smaller creeks not visible on most maps, or ephemeral streams, or even streams that have changed course since the data collection. In some cases, the coordinates may be slightly off, the result of over a century of data collection using a variety of methods, formats and record keeping. My methodology takes all of this into account by assigning each eel sample (point data) to a subwatershed that drains to specific pour points at the mouth of the Chesapeake Bay. This way, whether the fish appear to be on land or water, the model can determine the route these eels used to arrive at that point and what kind of barriers they may have encountered along their way.

In many cases however the eels that appear to be over land are actually in small streams and creeks that do not appear on the map. For example, two eels from tributaries on the York River appear to have been caught over land (Fig. 12A). When these locations are analyzed on Google Earth, they align with small streams (< 10 m wide). These streams are not visible in the most recent Google Earth imagery from May 2018 (Fig. 12B) but can be seen on earlier imagery from April 2013 (Fig. 12C-D).

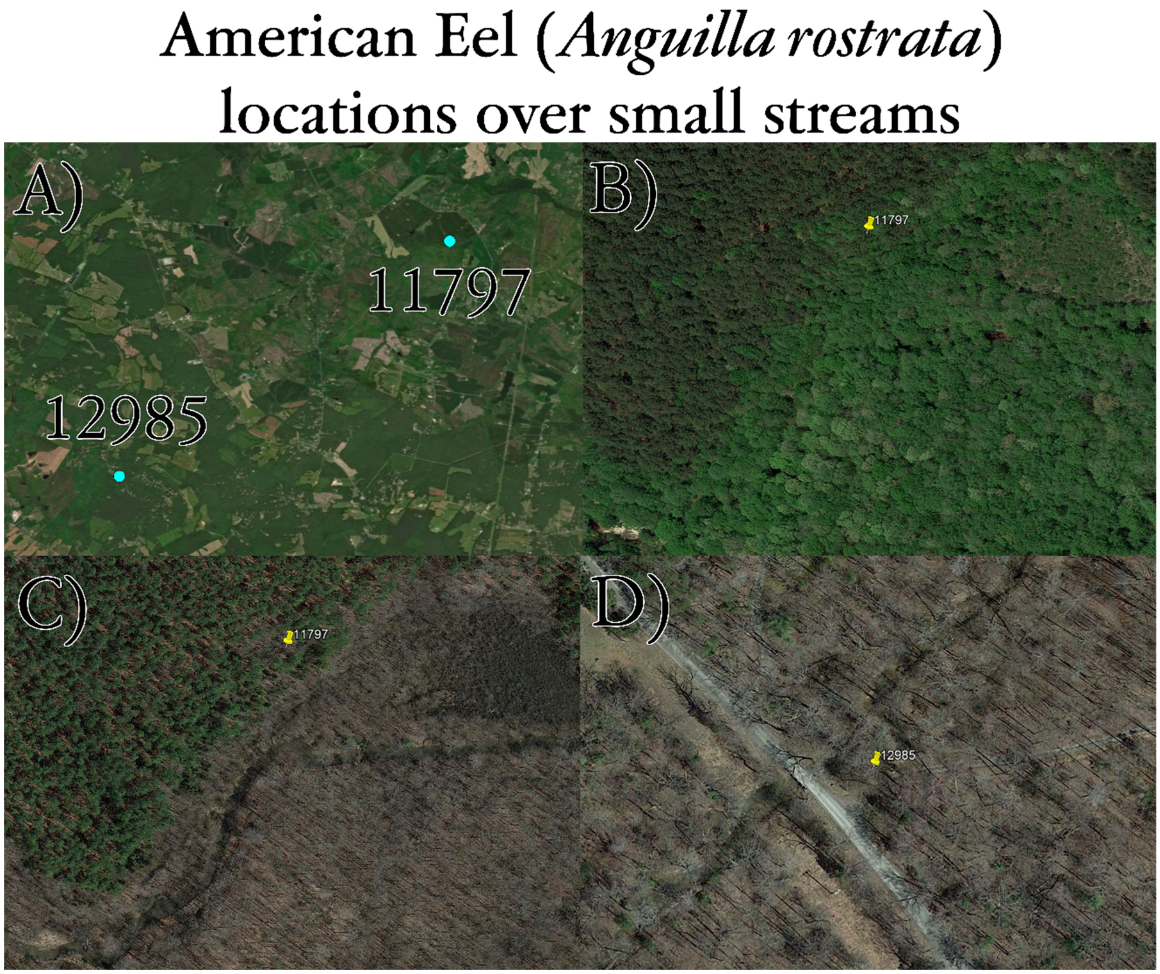

Fig. 12. Eel locations coincident with small streams not visible on the stream map. A) shows both locations (on tributaries of the York River) on the ArcGIS map. Location 11797 (37.926093 N, 77.801595 W) indicates three eels caught at Long Creek along Route 665 in Virginia on August 17, 1998, collection by D. Fowler and B. Mehl as part of the Warm Water Stream Survey. B) shows location 11797 in May 2018, when the stream was not visible. C) Shows the same location in April 2013. D) Location 12985 (37.877713 N, 77.869453 W, also shown in April 2013) indicates four eels caught by Marcel Montane (VDGIF) on August 31, 1988. Location numbers are based on their row number in the database.

The land use raster dataset was cropped to the study area using the “Extract by Mask” function. Land use resolution was 300 m^2. The raster originally contained twenty categories for land use, which were reduced to four for purposes of analysis using the *Reclassify* (Spatial Analyst) tool in ArcGIS. Areas marked “water bodies’ or “no data” (i.e.

no land at that point) were reclassified as water. Areas marked “urban areas” were left as-is. Areas labeled “Cropland” and “Bare areas” were reclassified to one category called “cropland/barren”. All other categories, which included “Herbaceous cover”, “Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)”, “Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)”, “Tree cover, broadleaved, deciduous, closed to open (>15%)”, “Tree cover, broadleaved, deciduous, closed (>40%)”, “Tree cover, needle leaved, evergreen, closed to open (>15%)”, “Tree cover, needle leaved, deciduous, closed to open (>15%)”, “Tree cover, mixed leaf type (broadleaved and needle leaved)”, “Mosaic tree and shrub (>50%) / herbaceous cover (<50%)”, “Mosaic herbaceous cover (>50%) / tree and shrub (<50%)”, “Shrubland”, “Grassland”, “Sparse vegetation (tree, shrub, herbaceous cover) (<15%)”, “Tree cover, flooded, fresh or brackish water”, “Shrub or herbaceous cover, flooded, fresh/saline/brackish water” were reclassified as “forests, shrubs and mosaics”. While there are likely large differences between these areas, determining the effects of things like deciduous forest buffers vs. evergreen forest buffers on American Eel is beyond the scope of this article.

To analyze the variables of eel density, dam density and land use I created a ranking system from 0-3 for each variable. Eel and dam densities were calculated by their abundance in the subwatershed segments (43 in total) divided by the total area of each segment. Eel data were tabulated by adding up the segments upstream to downstream, on the assumption that if an eel was found upstream it would have had to swim through the downstream sections to reach that location. So, the eel density numbers for the lowest reach of the Potomac River includes all sections above it. Eel density data (km^{-2}) were classified into four categories ranked lowest to highest: <1.0, ≥1 to 2, >2 to 5and >5. Dams were calculated in the opposite order, downstream to upstream, because to get to the upper reaches of a river an eel would have to pass through the downstream sections first. Dam densities (100 km^{-2}) were classified by subdividing the datasets to get a more or less even distribution of each of the four categories ranked highest to lowest: < 1, ≥1 to < 2, 2 to < 5 and ≥ 5 (Table 2). The methodology is illustrated (Fig. 13). The limitation to this method is that many of the dams are not on the mainstems of the rivers so an eel traveling upstream could swim pass them, but it provides a baseline of the difficulty of each section.

Table 2. Categories for each variable and their assigned rankings

Ranking	0	1	2	3
Eel density (km^{-2})	< 1.0	≥ 1.0 to <2.0	≥2 to 5	> 5
Dams w/o fish passage (100 km^{-2})	≥ 5	2 to < 5	1 to < 2	< 1
Land use	Urban areas	Cropland/barren	Forest, shrubs and mosaics	Water

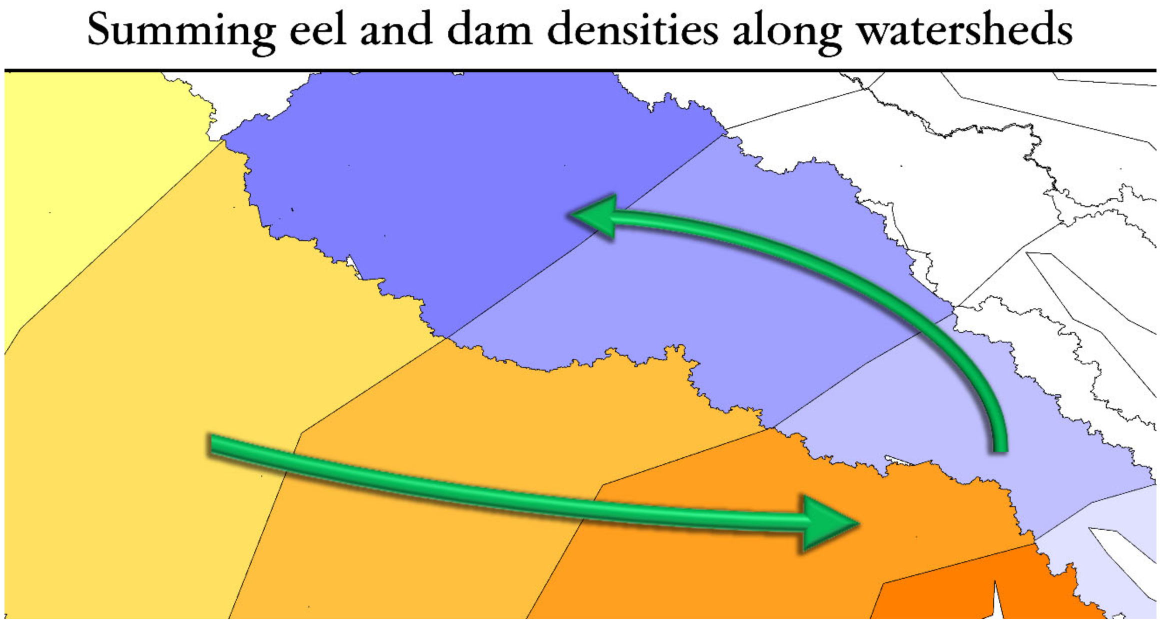

Fig. 13. The methodology for adding data along watersheds. Eel data are summed upstream to down (orange). Dam density data are summed downstream to up (lavender/blue).

The subwatershed polygon colors were adjusted using the *Symbology* tab in ArcGIS. By using the option to show *Unique Values* and a color ramp that runs from red to blue, new feature classes were generated from two value fields: eel density and dam density. These were converted from shapefiles to rasters using *Feature to Raster* (Conversion). This was not necessary for land use because it was already in raster format.

Each variable (eel density, dam density and land use) has four possible values (0-3), thus each raster has 4 colors. With two variables there are 16 possible values (4^2) and with three variables there are and 64 (4^3) possible values, which can be represented as 4-bit (2^4) or 6-bit (2^6) rasters. Simply summing the rasters together however will not produce this range of values, because the numbers will overlap and even combining all three layers will produce only 10 possible outcomes (0-9). Thus, the eel and dam density rasters were weighted using the *Reclassify* function to 1) account for the importance of each variable and 2) to increase the color depth of the output rasters.

Eel density is considered the most important variable, because if eels were found then by definition the area is habitable by eels. Dams are second, because barriers that physically block fish passage have been found to have a greater impact on eel abundance and density than urbanization (Machut et al., 2007). Eel density was reclassified by multiplying the values by 16 (2^4) and dam abundance was reclassified by a factor of 4 (2^2). This should not be interpreted as dams having exactly four times the importance of land use and eel abundance having four times the importance of dams. These numbers are used so that each combination of variables produces a unique value with no overlaps, thus maximizing the color depth of the raster when combining variables (in the case of three variables, it results in more than a six fold increase). All of the possible values are represented in a binary matrix (Table 3). To the best of our knowledge, this is the first study to sum multiple 2-bit rasters as binary numbers to generate a color palette for visual representation of data. Rasters were summed together using the *Cell Statistics* function (Spatial Analyst) in ArcGIS.

Table 3. Matrix of values for each combination of rankings of eel density, dam density and land use. With all three variables, each possible combination produces a unique value from 0 to 63, based on a 6-bit binary number. When dam density and land use rankings are used without eel density, only the first 16 rows (0-15) are used. When only eel and dam densities are used, the possible values are 0, 4, 8, 12, 16, 20, 24, 28, 32, 36, 40, 44, 48, 52, 56 and 60.

Rankings			Binary digit						Decimal
Eels km^{-2}	Dams 100 km^{-2}	Land use	32	16	8	4	2	1	
0	0	0	0	0	0	0	0	0	0
		1	0	0	0	0	0	1	1
		2	0	0	0	0	1	0	2
		3	0	0	0	0	1	1	3
	1	0	0	0	0	1	0	0	4
		1	0	0	0	1	0	1	5
		2	0	0	0	1	1	0	6
		3	0	0	0	1	1	1	7
	2	0	0	0	1	0	0	0	8
		1	0	0	1	0	0	1	9
		2	0	0	1	0	1	0	10
		3	0	0	1	0	1	1	11
	3	0	0	0	1	1	0	0	12
		1	0	0	1	1	0	1	13
		2	0	0	1	1	1	0	14
		3	0	0	1	1	1	1	15
1	0	0	0	1	0	0	0	0	16
		1	0	1	0	0	0	1	17
		2	0	1	0	0	1	0	18
		3	0	1	0	0	1	1	19
	1	0	0	1	0	1	0	0	20
		1	0	1	0	1	0	1	21
		2	0	1	0	1	1	0	22
		3	0	1	0	1	1	1	23
	2	0	0	1	1	0	0	0	24
		1	0	1	1	0	0	1	25
		2	0	1	1	0	1	0	26
		3	0	1	1	0	1	1	27
	3	0	0	1	1	1	0	0	28
		1	0	1	1	1	0	1	29
		2	0	1	1	1	1	0	30
		3	0	1	1	1	1	1	31
2	0	0	1	0	0	0	0	0	32
		1	1	0	0	0	0	1	33
		2	1	0	0	0	1	0	34
		3	1	0	0	0	1	1	35

	1	0	1	0	0	1	0	0	36
		1	1	0	0	1	0	1	37
		2	1	0	0	1	1	0	38
		3	1	0	0	1	1	1	39
	2	0	1	0	1	0	0	0	40
		1	1	0	1	0	0	1	41
		2	1	0	1	0	1	0	42
		3	1	0	1	0	1	1	43
	3	0	1	0	1	1	0	0	44
		1	1	0	1	1	0	1	45
		2	1	0	1	1	1	0	46
		3	1	0	1	1	1	1	47
3	0	0	1	1	0	0	0	0	48
		1	1	1	0	0	0	1	49
		2	1	1	0	0	1	0	50
		3	1	1	0	0	1	1	51
	1	0	1	1	0	1	0	0	52
		1	1	1	0	1	0	1	53
		2	1	1	0	1	1	0	54
		3	1	1	0	1	1	1	55
	2	0	1	1	1	0	0	0	56
		1	1	1	1	0	0	1	57
		2	1	1	1	0	1	0	58
		3	1	1	1	0	1	1	59
	3	0	1	1	1	1	0	0	60
		1	1	1	1	1	0	1	61
		2	1	1	1	1	1	0	62
		3	1	1	1	1	1	1	63

To calculate CPSE within the study area, I filtered the eel data by removing any fish identified as glass eels or elvers (which are much smaller and thus likely to be caught in higher numbers than yellow or silver eels) and removed any counts >99 at a given sample point, because these may have also represented unlabeled glass eels/elvers. This created a subset of 70,794 eels, which I then identified by subwatershed by using the Clip (Analysis) tool in ArcGIS. The totals in each subwatershed were divided by the count (rows) and the mean value was considered the CPSE. CPSE was compared to eel and dam density using scatterplots and linear regression.

Results

Based on the Digital Elevation Model data, I created 24 subwatersheds (Table 4).

Table 4. Names and locations of subwatersheds

ID	Watershed	Number of segments	Pour Point	
			Latitude	Longitude
01	Chester River	1	39.10246025	-76.12470255
02	Choptank River	2	38.65775045	-76.2594917
03	East Bay	1	38.87024801	-76.28267779
04	Elk River	1	39.49985739	-75.92311147
05	Gunpowder River	1	39.3561245	-76.328986
06	James River	5	36.95954424	-76.38666492
07	Manokin River	1	38.1428192	-75.81854124
08	Nanticoke River	1	38.27483653	-75.93012284
09	North East River	1	39.5659299	-75.9753457
10	Patapsco River	2	39.24754951	-76.6067941
11	Patuxent River	3	38.31011755	-76.42320815
12	Penny Creek	1	37.838498	-76.321963
13	Piankatank River	1	37.53376757	-76.40100119
14	Pocomoke River	1	37.97033781	-75.64453153
15	Potomac River	6	37.99001043	-76.35477766

16	Rappahannock River	4	37.59753491	-76.39368687
17	Romney Creek	1	39.38837975	-76.22281121
18	Sassafras River	1	39.381081	-75.905276
19	Severn River	1	38.98637424	-76.47933093
20	Susquehanna River	1	39.5435853	-76.07998685
21	Swan Creek	1	39.48654066	-76.12392089
22	Transquaking River	1	38.36873778	-76.00049124
23	Wicomico River	1	38.276365	-75.776396
24	York River	4	37.23746834	-76.39808724
	Total segments:	**43**		

The watersheds labeled by their ID numbers are shown (Fig. 14).

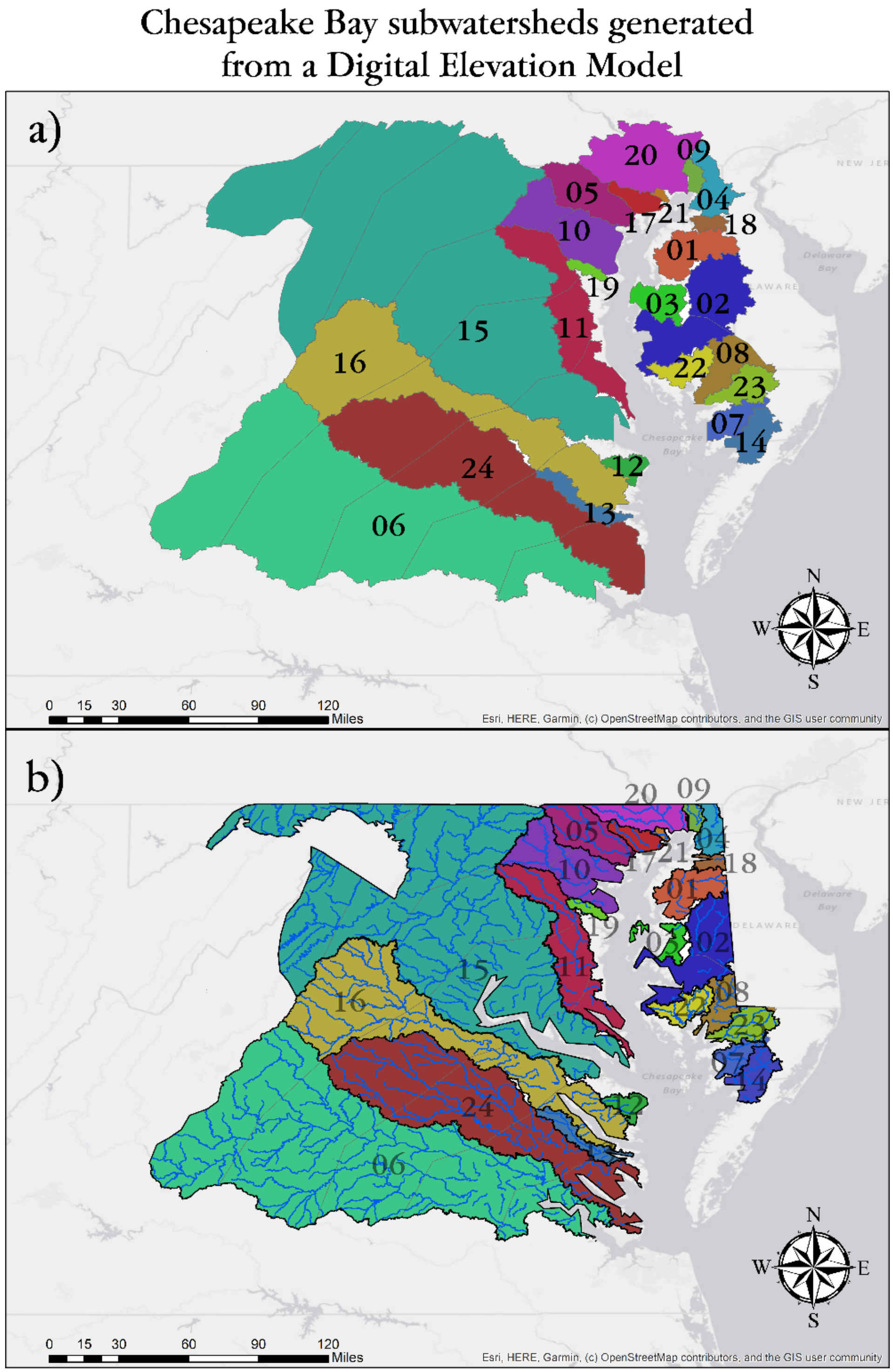

Fig. 14. Subwatersheds created from a Digital Elevation Model (DEM). 14a shows the watersheds labeled by the ID numbers in Table 4. 14b shows the watersheds after being clipped to the boundaries of Virginia, Maryland and Washington, D.C., with rivers based on the DEM data. Not all rivers and tributaries are shown.

Delineating the watersheds at approximately 50 km along the mainstem resulted in multiple segments for six of the rivers and 43 segments in total. Segment 01 starts at the mouth of the river where it enters the Chesapeake Bay and the numbers increment from downstream to upstream (Table 5).

Table 5. Area (km^2), eel density (km^{-2}), dam density ($100\ km^{-2}$) and rankings for each subwatershed segment

			Density		Ranking	
Subwatershed	**Segment**	**Area (km^2)**	**Eels km^{-2}**	**Dams $100\ km^{-2}$**	**eels**	**dams**
Chester River		1,423.40	3.04	6.88	2	1
Choptank River	01	1,349.72	2.85	0.44	2	3
	02	1,565.65	1.06	1.28	1	2
East Bay		513.82	3.87	0.39	2	3
Elk River		699.46	1.88	1.72	1	2
Gunpowder River		1,867.78	0.75	0.96	0	3
James River	01	1,853.82	65.59	1.73	3	2
	02	4,227.82	1.56	2.63	1	1
	03	5,455.68	0.55	7.97	0	0
	04	7,922.56	0.28	9.19	0	0
	05	6,903.82	0.13	14.02	0	0
Manokin River		623.30	0.27	0.00	0	3
Nanticoke River		883.09	2.43	0.34	2	3
North East River		262.91	2.16	1.14	2	2
Patapsco River	01	1,683.54	1.52	1.72	1	2
	02	1,267.88	0.23	2.37	0	1
Patuxent River	01	802.028	4.83	3.12	2	1
	02	1,613.42	1.73	3.66	1	2
	03	1,500.88	1.11	7.13	1	0
Penny Creek		459.431	0.80	0.22	0	3
Piankatank River		756.64	1.20	1.59	1	2
Pocomoke River		963.80	0.12	0.00	0	3
Potomac River	01	1,803.63	41.69	0.83	3	3
	02	5,407.11	13.56	1.65	3	2
	03	6,548.17	9.99	4.58	3	1
	04	7,688.27	8.14	4.99	3	1
	05	4,502.58	13.75	9.44	3	0
	06	1,493.13	0.13	3.15	0	1

Rappahannock River	01	1,419.63	34.91	1.48	3	2
	02	1,689.84	5.65	3.25	3	1
	03	1,816.19	2.50	5.07	2	0
	04	5,748.13	0.24	4.05	1	1
Romney Creek		550.26	3.35	0.91	2	3
Sassafras River		250.36	12.12	8.39	3	0
Severn River		256.05	4.24	5.47	2	0
Susquehanna River		1,316.92	3.92	2.05	2	1
Swan Creek		79.75	6.28	0.00	3	3
Transquaking River		809.49	0.69	0.25	0	3
Wicomico River		963.319	0.63	2.18	0	1
York River	01	1,426.64	631.85	2.10	3	1
	02	1,946.95	4.25	4.16	3	1
	03	3,892.30	2.02	5.60	2	0
	04	4,383.26	0.89	7.67	0	0
	Total	**98,952.41**				

* The very high numbers for eel densities on the lower reaches of the James and York rivers reflects glass eel surveys in these areas between 2000 and 2009.

There were 1,184,141 eels sampled in the study area. The eels clipped to the study area are shown (Fig. 15).

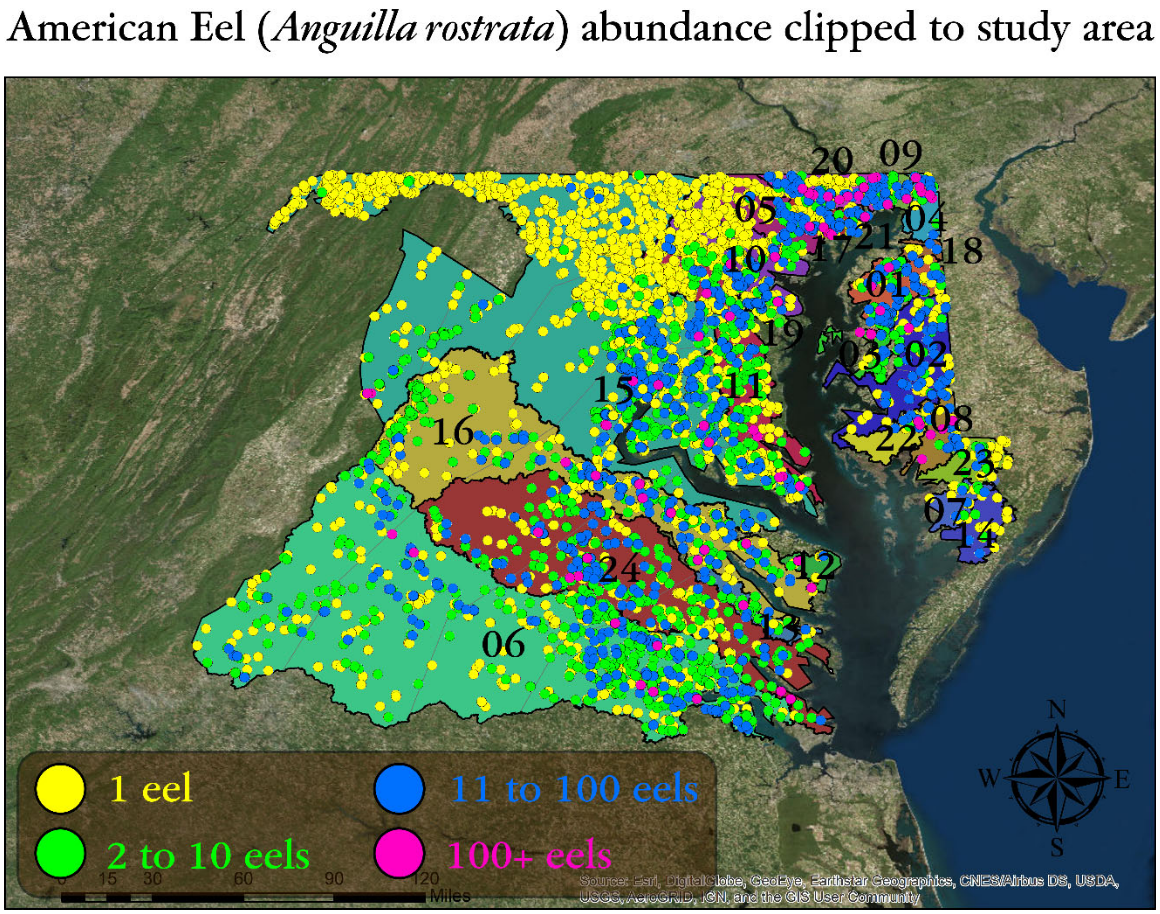

Fig. 15. American Eel (*Anguilla rostrata*) abundance data clipped to the study area of Chesapeake Bay subwatersheds. Yellow circles represent individual eels, green 2 to 10 eels, blue 11 to 100 and magenta 100 or more. Numbers correspond to watershed labels in Table 4.

The study area had 2,435 dams, with 30 (1.23%) having provisions for fish passage (Fig. 16). The date of construction was available for 913 of the dams. In the study area, all dams were built between 1800 and 2001 (Fig. 17) and the highest years of dam construction were from 1955 to 1975, with an average of 26 dams built per year during these two decades (Fig. 18). The graph does not include records of any dams that were removed.

Locations of dams within the study area

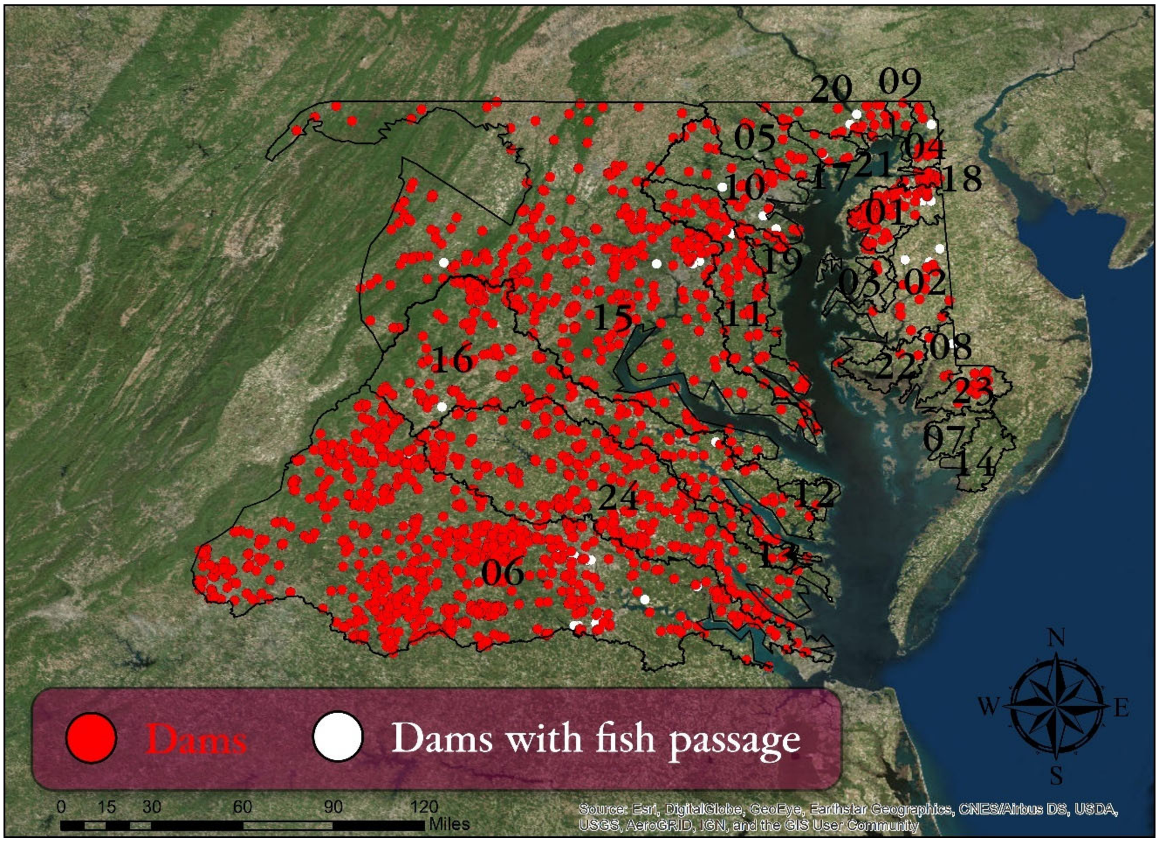

Fig. 16. Locations of dams in the study area (Chesapeake Bay subwatersheds). Red dots indicate dams without fish passage; white dots indicate dams with upstream fish passage. Numbers correspond to the watershed labels in Table 4.

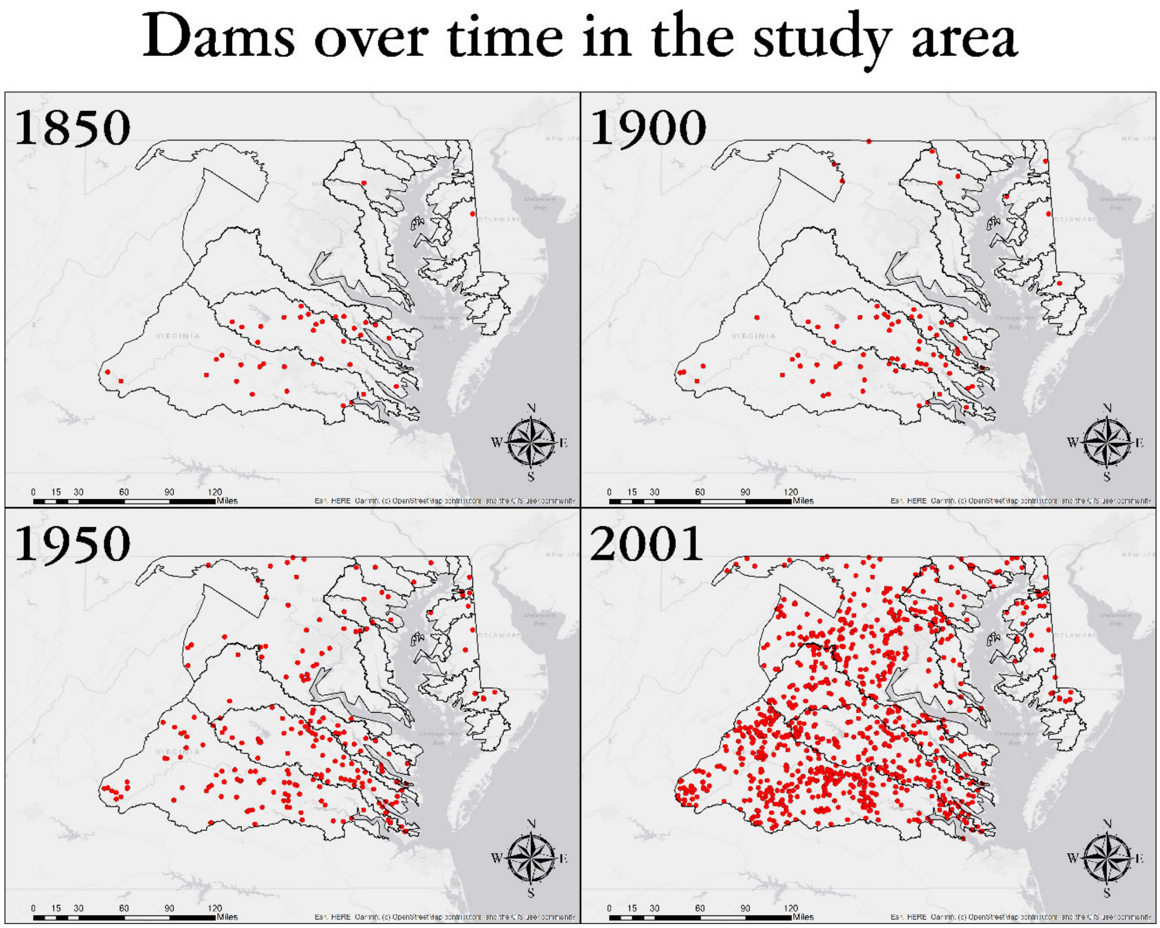

Fig. 17. Dams over time in the study area (Chesapeake Bay subwatersheds) for the 913 dams for which date of construction was available.

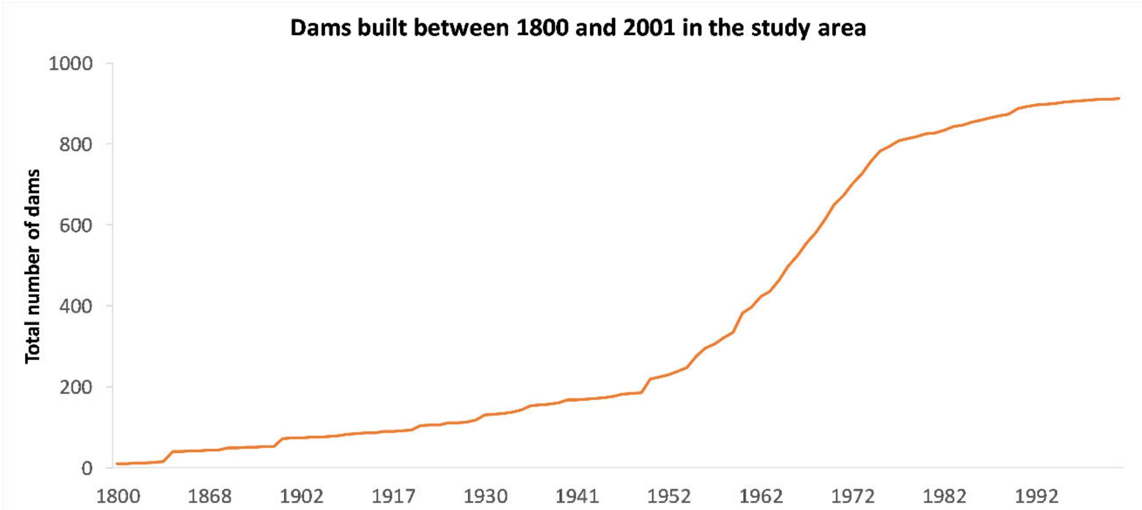

Fig. 18. Construction of dams in the study area (Chesapeake Bay subwatersheds) from 1800 to 2001 for the 913 dams where the date constructed was known. Note years of peak construction between 1955-1975.

The results for eel density, dam density and the combination of these variables are shown (Fig. 19).

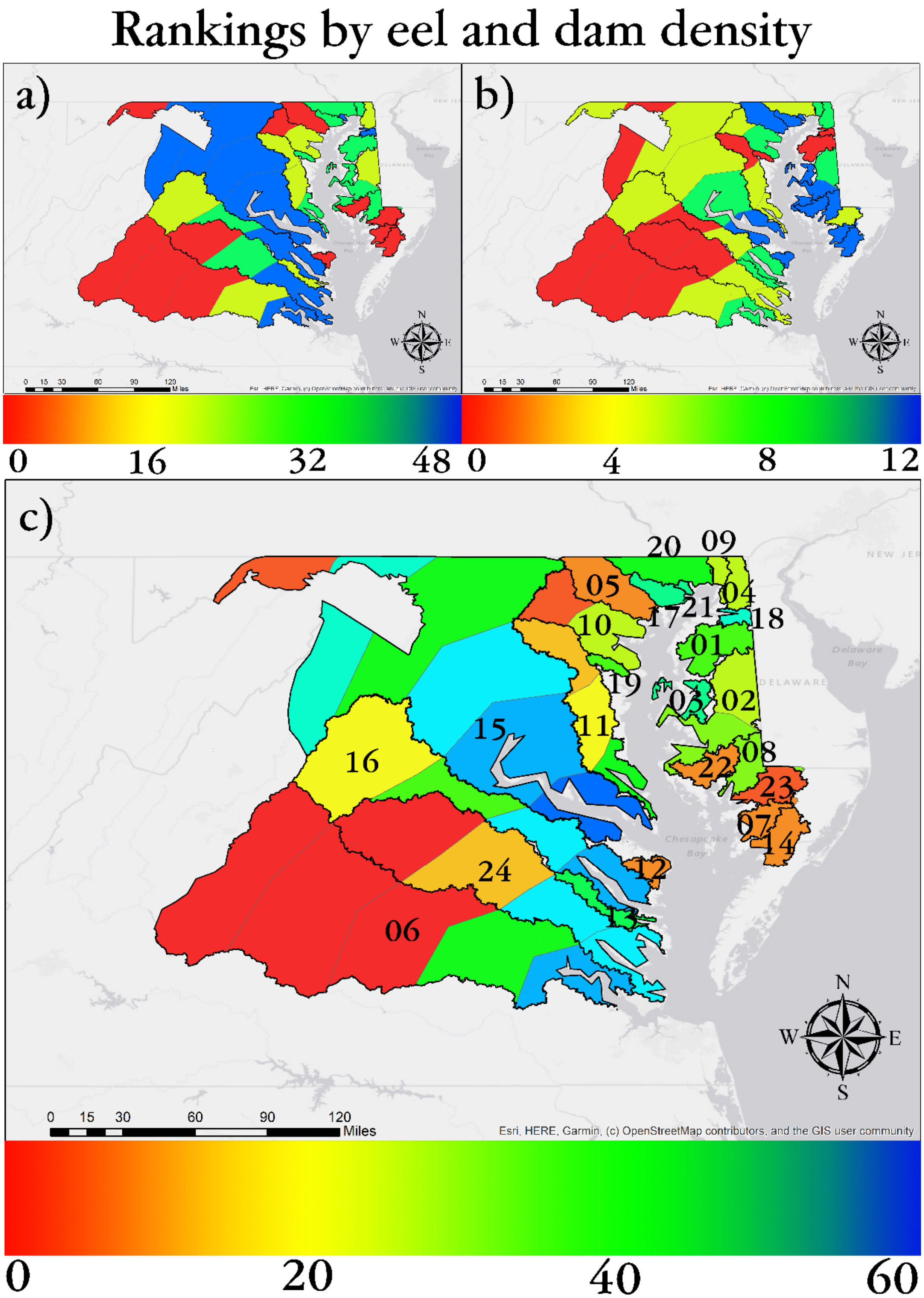

Fig. 19. 19a shows eel density, 19b shows dam density and 19c and shows the combined dam and eel density rankings. Color ramp indicates rankings from low (red) to high (blue). Numbers on color ramps correspond to values in Table 3. Numbers over watersheds correspond to labels in Table 4.

The reclassified land use data for the study area is shown (Fig. 20). Most (88.96%) of the land within 2 km of the rivers was classified as category 2 – forests, shrubs and mosaics, followed by urban areas (5.44%), water (4.87%) and cropland/barren (0.73%).

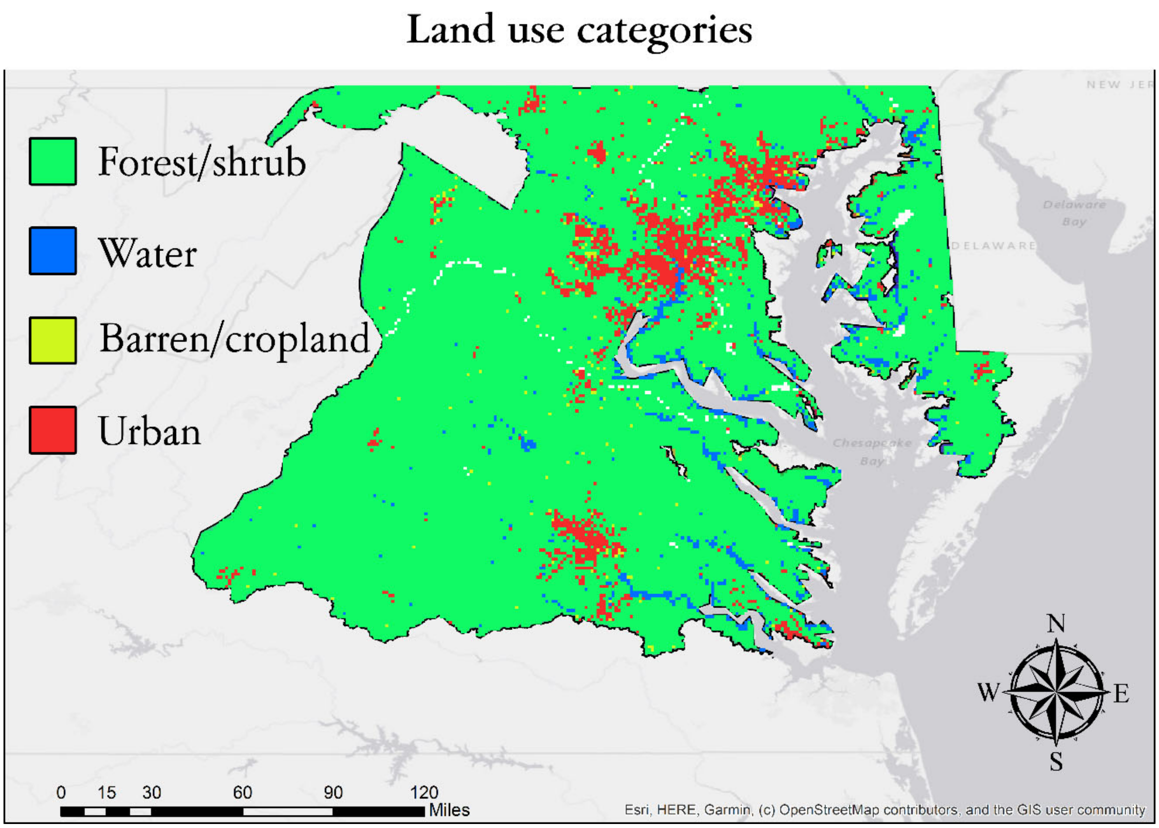

Fig. 20. Green indicates areas with plant cover, blue represents water, yellow barren surfaces/cropland only and red urbanized areas. Red primarily corresponds to the three metropolitan areas on the map, Baltimore Maryland, Washington D.C. and Richmond Virginia.

Combining the rasters for dams and land use produces a 4-bit raster with 16 possible values for each pixel. Areas in blue indicate few barriers and good land use values while areas in red indicate areas with more barriers and impervious surfaces or barren areas. The combined dam and land use data are shown (Fig. 21).

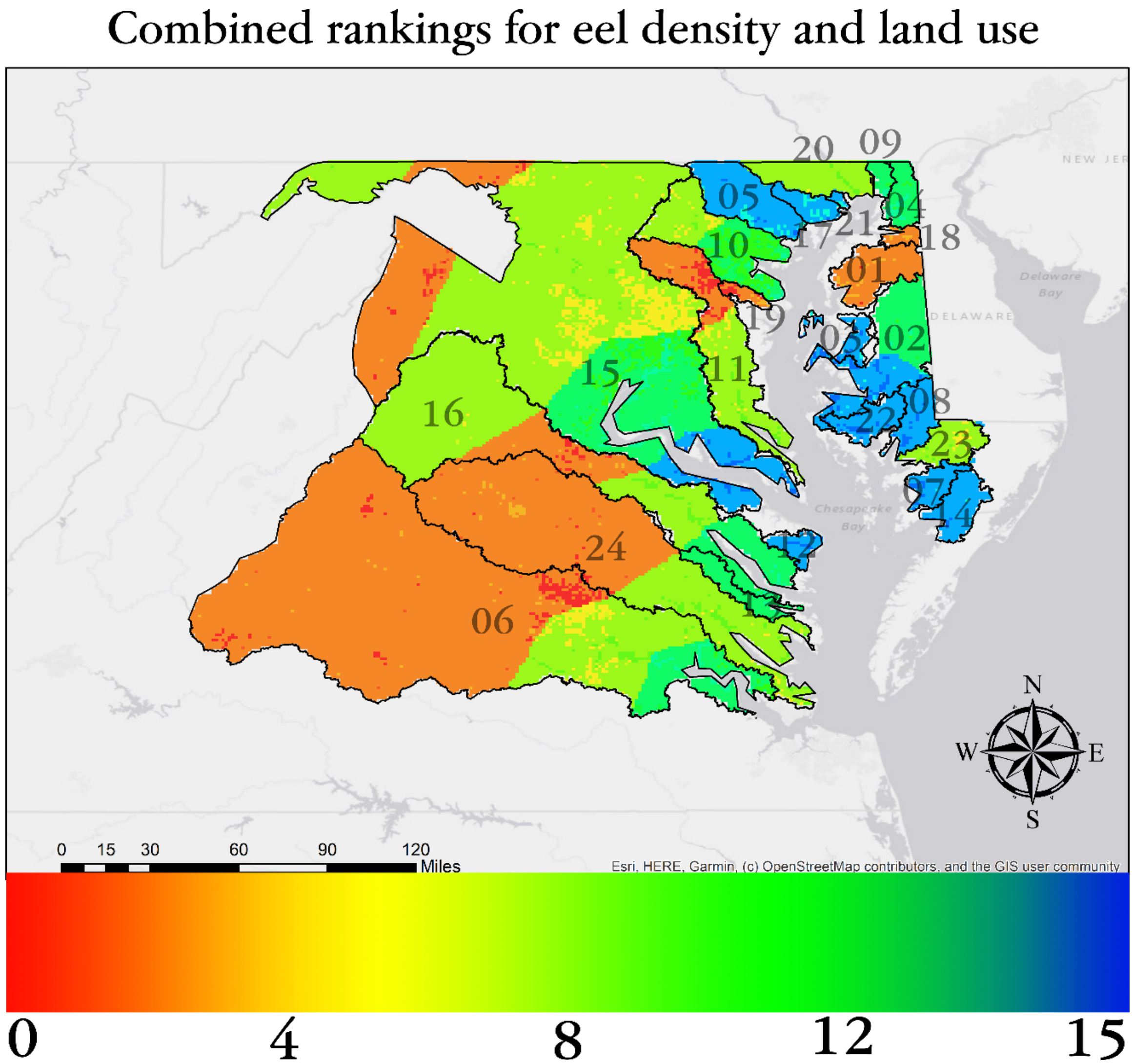

Fig. 21. A "features only" map combining the rankings for dam density and land use. The scale runs from blue (highest-ranked areas with fewer dams and higher ranking land use categories) to red (lowest-ranked areas with more dams and lower ranking land use categories). As shown in Table 3, potential values range from 0 to 15. Numbers correspond to watershed labels in Table 4.

The stream boundaries, generated from the DEM (dark blue lines) and the USGS data (with a 2 km polygon around the polylines) are shown (Fig. 22).

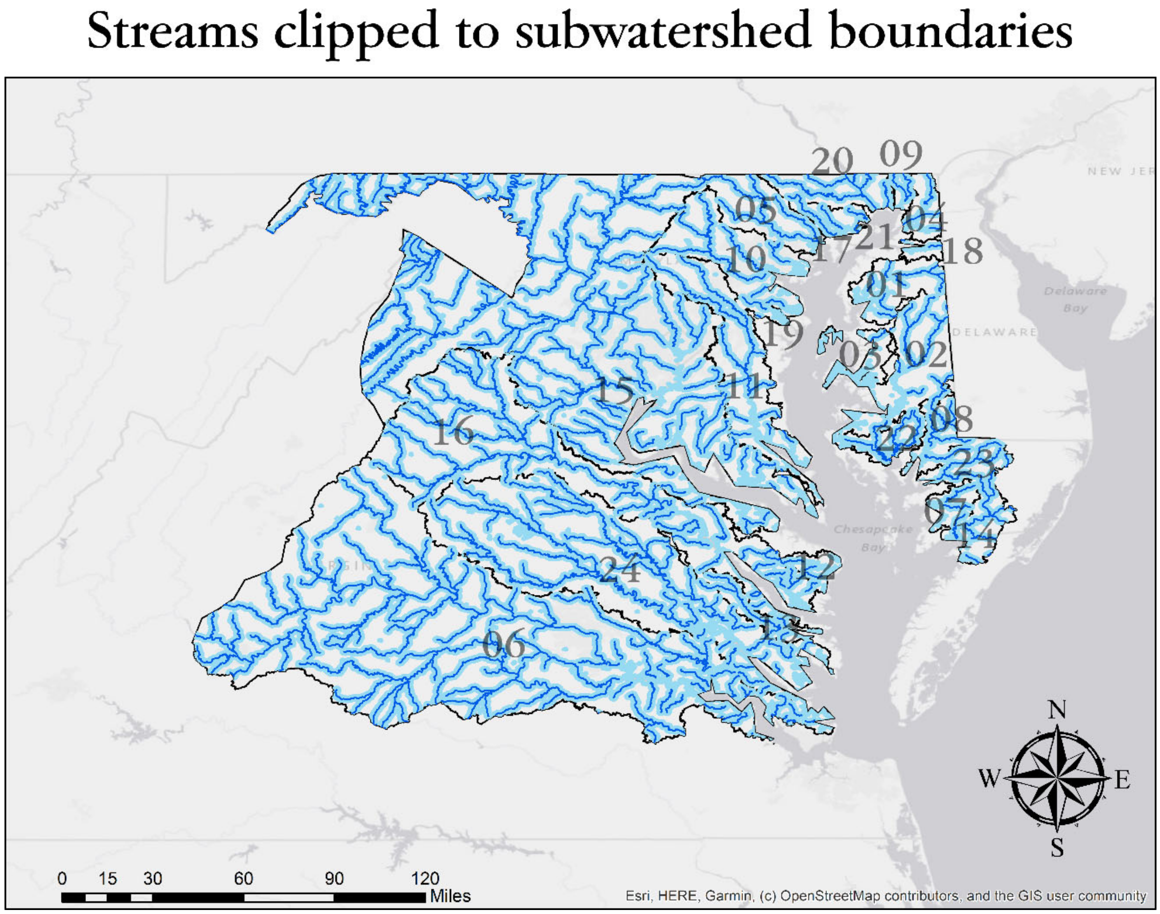

Fig. 22. Streams clipped to watershed boundaries. The darker blue lines are generated from the Digital Elevation Model (DEM), while the lighter blue lines are a combination of the USGS imagery, the DEM and a 2 km polygon around the polylines. Numbers correspond to watershed labels in Table 4.

When the three layers (eel density, dam density and land use) are added together, the result is a 6-bit (64 possible colors) raster. This raster was extracted from the stream boundary mask to produce Fig. 23.

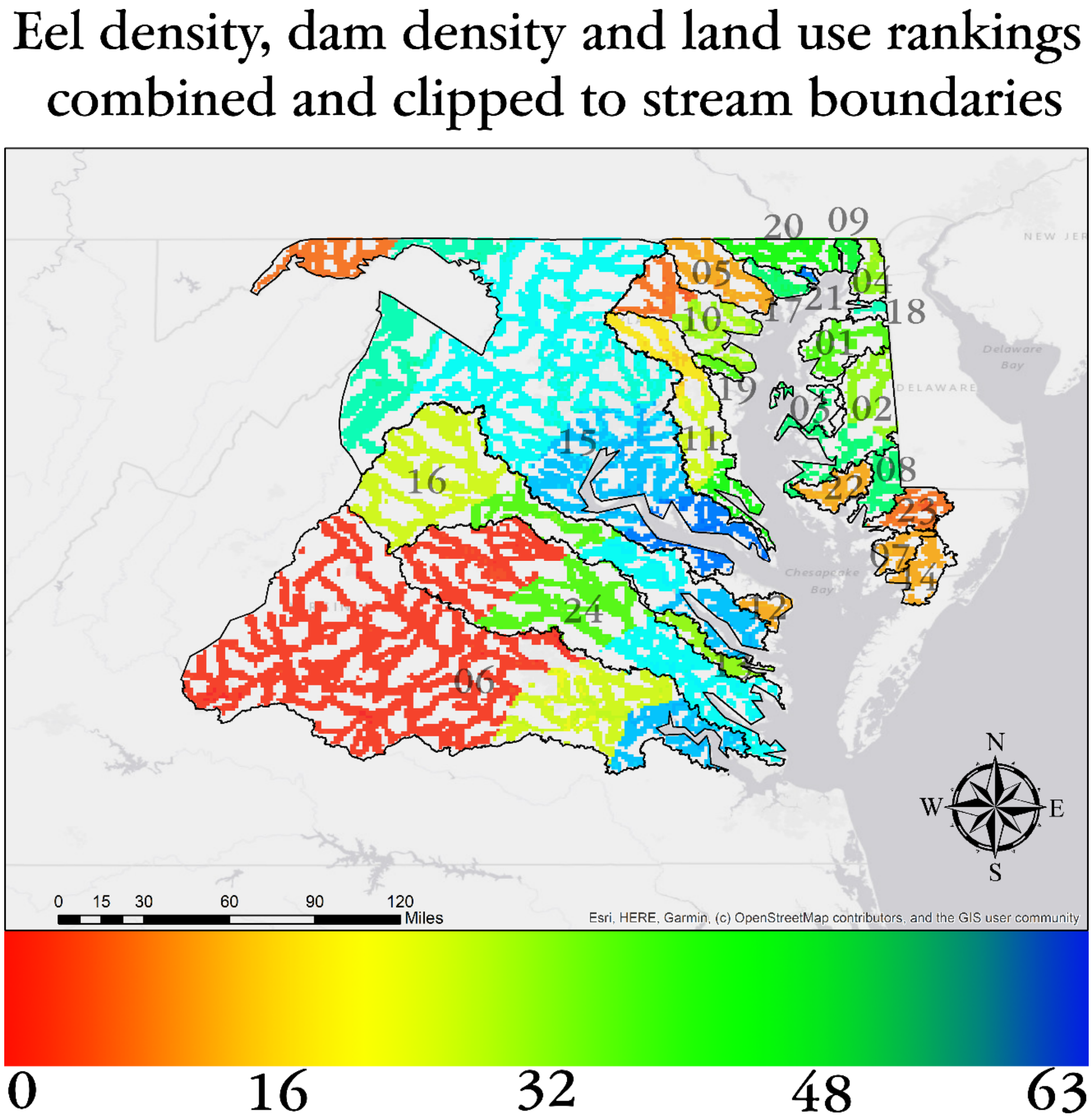

Fig. 23. Map combining the rankings for eel density, dam density and land use, clipped to river boundaries. The color bar runs from red (lowest-ranked areas) to blue (highest-ranked areas) with values from 0 to 63. Numbers correspond to watershed labels in Table 4.

CPSE varied by watershed and segment. The average CPSE was 7.78, with a standard deviation of 4.88. The lowest value was 1.05, at Potomac River 06 and the highest value was 23.38 at York River 01. CPSE values per watershed are shown (Fig. 24). CPSE was compared to the density of yellow/silver stage eels (Fig. 25) and to the density of dams (Fig. 26) per subwatershed segment.

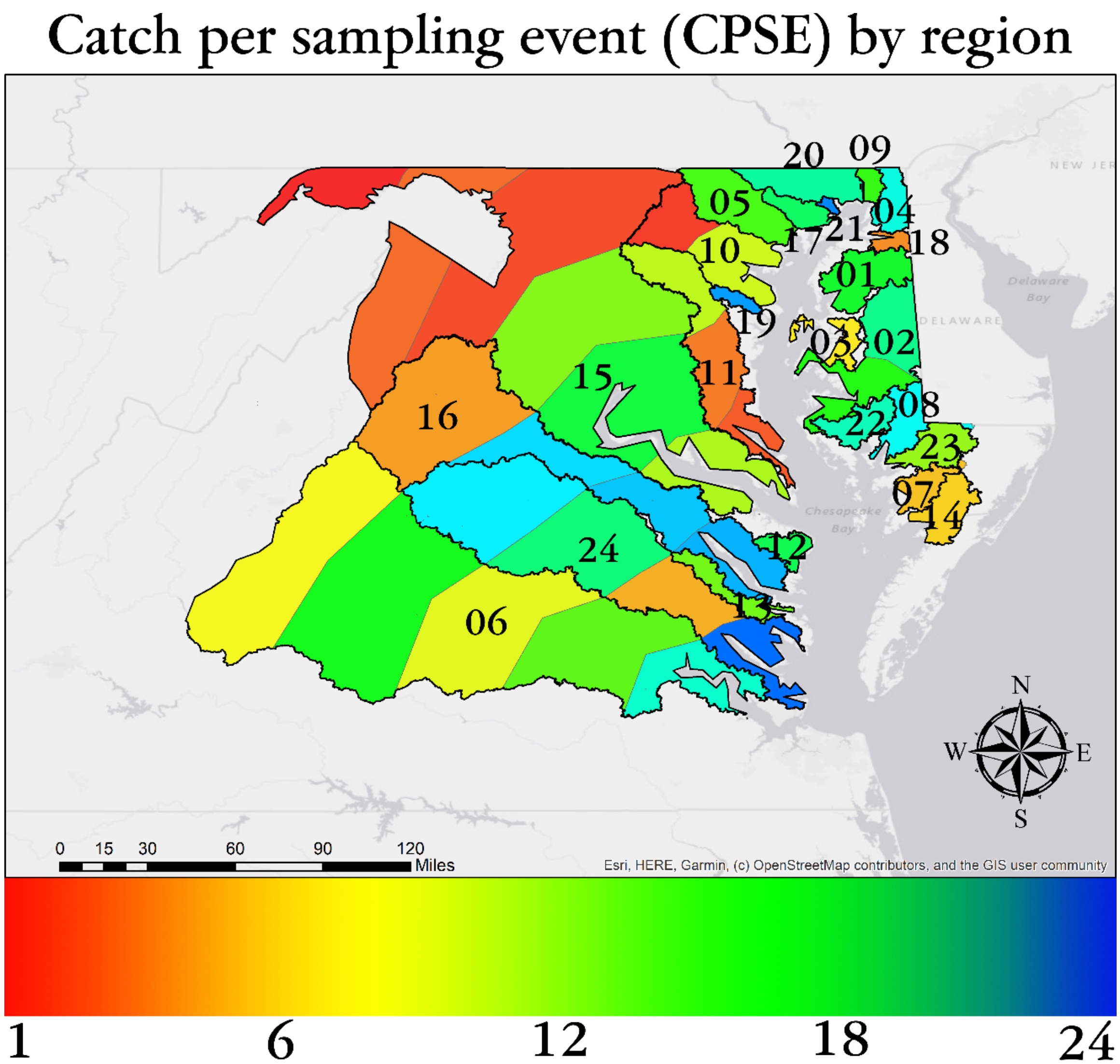

Fig. 24. Catch per sampling event (CPSE) for all watershed segments. Values range from red (low) to blue (high). Colors correspond to the CPSE values themselves rather than rankings. Numbers correspond to watershed labels in Table 4.

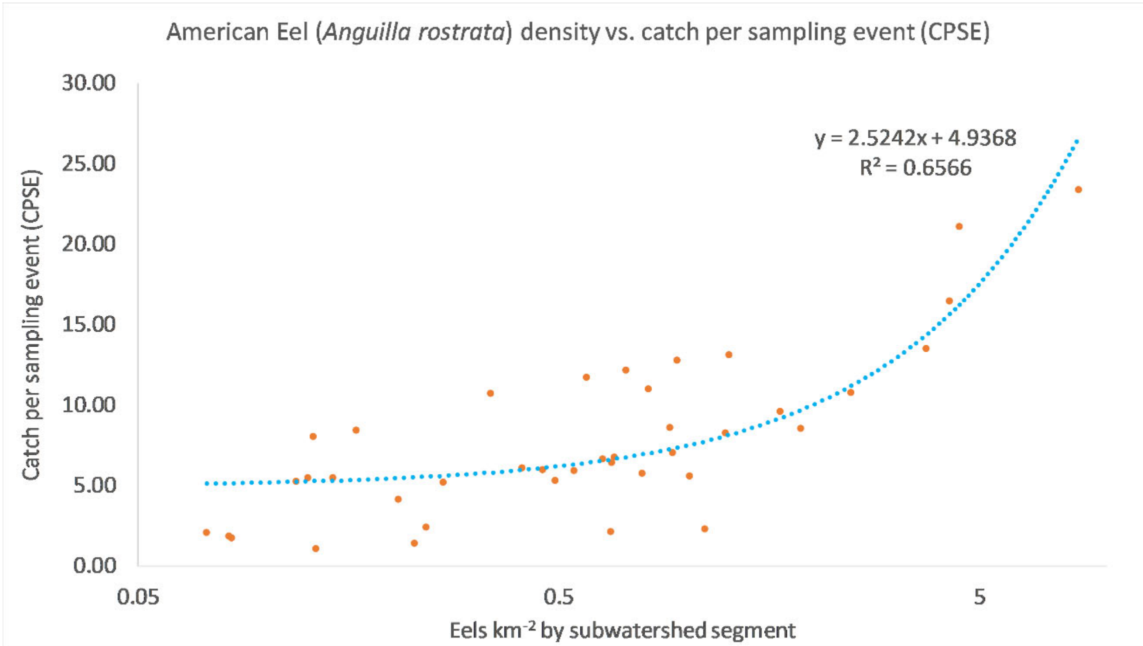

Fig. 25. Yellow and silver stage American Eel (*Anguilla rostrata*) density vs. Catch per sampling event (CPSE) by subwatershed segments. The dot in the upper right corner is York River 01, which had the highest eel density (8.62) and the highest CPSE (23.38). Trendline is based on linear regression.

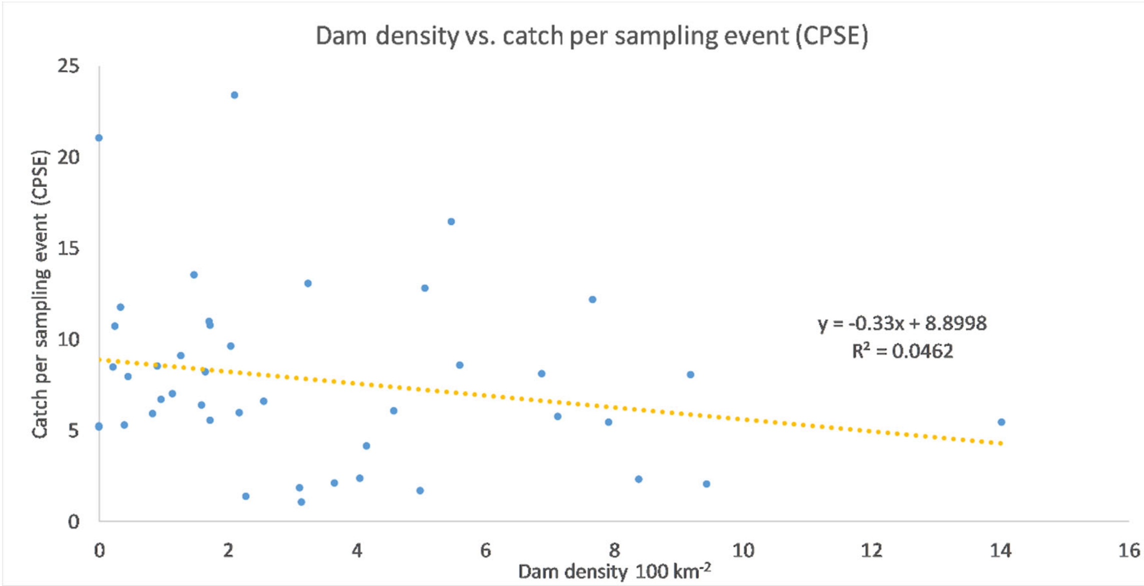

Fig. 26. Dam density (100 km^{-2}) and catch per sampling event per watershed. Trendline is based on linear regression.

Discussion

The primary limitation to this study is that the eel data collection records are not consistent by region and CPSE presents its own limitations. Thus, based on results I cannot definitively say if one river or segment has a higher eel density than another and areas in red should be considered candidates for further study rather than places where eels are disappearing. The eel numbers are baseline records of what has been documented, thus a river that appears to have low eel density could potentially improve with more consistent sample methods. On the other hand, areas with relatively high densities however can be considered as places where eels appear to be doing well. Additionally, the dam density and land use data can be used to determine eel habitat suitability.

One benefit to dividing the rivers into segments and adding eel abundance cumulatively to create the total eel densities is seen on the Potomac River, where the downstream locations do not have many documented eels but the numbers from the Shenandoah tributary (segment 05) make up for it. Thus, this methodology goes beyond tallying eel counts in a localized area and shows how sampling in one place can affect the ranking of an area 200 km away.

Based on the eel density layer only, the highest ranking (> 5 eels km^{-2}) were James River 01, Potomac River 01-05, Rappahannock River 01-02, Sassafras River, Swan Creek and York River 01-02. The lowest ranking (< 1.0 eels km^{-2}) areas were Gunpowder River, James River 03-05, Manokin River, Patapsco River 02, Penny Creek, Pocomoke River, Potomac River 06, Transquaking River, Wicomico River and York River 04. Two locations (James River 01 and York River 01) have very high eel densities because of glass eel surveys in these areas between 2000 and 2009. This however does not impair the accuracy of the results because these locations would have had the maximum value for eels (3) even without the glass eel counts.

Examining only the dam density layer, the highest ranked areas (dam density < 1 100 km^{-2}) were Choptank River 01, East Bay, Gunpowder River, Manokin River, Nanticoke River, Penny Creek, Pocomoke River, Potomac River 01-02, Romney Creek, Swan Creek and Wicomico River. Three of these locations (Manokin River, Pocomoke River and Swan Creek) had no dams in the study area. The areas with the highest dam densities (≥5 100 km^{-2}) were the Chester River, James River 03-05, Patuxent River 03, Potomac River 05, Rappahannock River 04, Sassafras River, Severn River and York River 03-04.

When the eel and dam data are combined, the areas of most concern are York River 04 (upstream of Cedar Fork, VA) and James River 03-05 (from the headwaters to Richmond), especially segment 05, which had the highest dam density (14.02 100 km^{-2}). Each of these areas had the lowest eel density rankings and the highest dam density rankings. Wicomico River and Patapsco River 02 also had the lowest rank for eel densities and second highest dam density ranking.

On the other hand, some areas appeared to be doing comparatively well. Potomac River 01 and Swan Creek each had the highest eel density ranking and the lowest dam density ranking. Swan Creek also had the second highest CPSE, 21.06, and was the only location besides York River 01 to have a CPSE >20. Potomac River 02, James River 01 and Rappahannock River 01 each had the highest eel density ranking and the second lowest dam density ranking. Potomac River 03, Rappahannock River 02 and York River 01-02 had the highest eel density ranking and the third lowest dam density ranking.

When eel density and CPSE were compared by watershed segments (Fig. 25), there is a positive relationship based on linear regression ($R^2 = 0.6566$). This could indicate the eel density data accurately reflects actual eel abundance, but without groundtruthing in the form of sampling eels in these areas using consistent gear and methodology, it is difficult to draw conclusions from these data. There may be a slight negative relationship between dam density and CPSE (Fig. 26) but further studies will be necessary to make this determination.

Based on these results, the Potomac River and Rappahannock River appear to be watersheds of lesser concern, although the Potomac River drops to a very low ranking at the upper reach (segment 06). This could be due to reduced sampling effort above segment 05, an area that was sampled many times by the USFWS, or it could be the result of the dams in segment 05 (9.44 100 km^{-2}). Yet another complication is that this section of the Potomac is missing large portions of the watershed in PA and WV, which are outside the study area. It would be beneficial to run this analysis including eel data from all Chesapeake Bay states and the full extent of the Potomac River before drawing conclusions on habitat suitability of the upper regions of this river. The James River and York River both start with good rankings for eel and dam densities near the Bay but end up with much lower scores further upstream, indicating the barriers may be affecting upstream eel densities.

The rankings for eels and dams do not correlate at most locations and are sometimes contradictory. For example, Gunpowder River, Manokin River, Penny Creek, Pocomoke River and Transquaking River all have very low eel densities despite also having low densities of dams. In these cases, the low eel densities could reflect a lack of sampling efforts in these locations, or it may indicate there are reasons other than dams for the low numbers. The latter explanation seems more likely for the Gunpowder River, Manokin River and Pocomoke River, since each location had below average CPSE, whereas Penny Creek and Transquaking River had above average CPSE.

On the other hand, Potomac River 05 and Sassafras River have very high eel densities while also having high dam densities, indicating that at least in some cases the dams are not acting as complete barriers to migration, which is supported by previous studies (Shepard, 2015b). This is especially interesting considering both locations have below average CPSE.

Land use was highly localized, with the majority of the urban areas (impervious surfaces) occurring in the metropolitan areas around Baltimore MD, Washington D.C. and Richmond, VA. These correspond to the subwatersheds of James River 02-03, Potomac River 02-03, Patuxent River 02-03, Severn River and Patapsco River 01.

Eel data is weighted more heavily than either of the other factors, because while stream connectivity and riparian buffers can help create potential habitat for eels, the density data itself shows places where eels may be present in spite of less than ideal environmental conditions. Another option could be to use CPUE data in future studies, although it has its own drawbacks since it can differ by gear type, which was not listed for ~75% of samples.

My recommendation for restoring the American Eel population is to 1) increase access to habitat by re-opening stretches of rivers by removing dams and barriers and 2) increase the quality of the habitat by restoring riparian buffers, which can limit eutrophication from run-off and provide cover for juvenile eels that prefer slower depositional areas with deciduous leaf litter for cover (Johnson, J. H. & Nack, 2013).

There are a variety of methods for prioritizing dam removal or fish passage facilities. The Freshwater Network, part of The Nature Conservancy, has built a map of dams organized by aquatic barrier prioritization for the Chesapeake Bay region (Network, 2019). A simpler method might be to start with the furthest dam downstream. For example on the Susquehanna River, improving passage at upstream dams without changing the initial dam did not significantly improve upstream eel densities (Sweka et al., 2014). For migrating salmon, the Washington State Fish & Wildlife Department uses criteria such as habitat suitability, production potential for adults, potential habitat gain, species mobility, species stock condition (whether or not the stock is "of concern" or "depressed") and potential costs (Kocovsky et al., 2009; Kocovsky et al., 2008). But since eels have the opposite migration patterns as salmon, this framework may not be completely applicable for conservation measures.

Whether a dam is removed, modified or kept depends on biological, social and economic factors. Dam removal results in hydrologic changes both up and downstream, such as sediment movement and deposition, which alter fine-scale habitat suitability (Kocovsky et al., 2009). As such, it may be useful to conduct pre-removal risk assessments, especially in areas where upstream sediments contain pollutants (Gregory et al., 2002). Dam removal can also be expensive and difficult (Lawson, 2016). Eel ladders are relatively cheap and can provide passage quickly (Schmidt et al., 2009) although they may not be ideal for most migratory fish (Day et al., 2012) An eel ladder retrofitted to a dam on the Shenandoah River is accessible to eels between 19 to 74 cm in length. It appears smaller eels are not able to ascend, but most in that size range have probably not yet metamorphosed to yellow eels and therefore are not migrating upstream (Welsh & Liller, 2013).

An additional benefit to improving access to upstream habitats for eels comes in the distribution of *Elliptio mussels.* Larvae of freshwater mussels (Bivalvia: Unionidae) are host-dependent and attach to fish hosts until they become free-living juveniles (Galbraith et al., 2018). The Eastern Elliptio Mussel, *Elliptio complanata*, uses American Eel as its primary fish host, but both species are in decline (Strayer & Malcom, 2012). In the Chesapeake Bay watershed, *E. complanata* recruitment is limited and this appears to be caused by host species distribution, since the mussels are much more abundant downstream of dams on the mainstem of the Susquehanna River than upstream (Galbraith et al., 2018). Restoring American Eel to a stream improves *E. complanata* recruitment but not consistently, since water quality (especially nitrogen and sedimentation) and habitat also play a role (Galbraith et al., 2018), which emphasizes the need to improve riparian buffers as well.

Eels can be restocked to areas but this is not a panacea since stocked individuals have different growth rates and sex ratios compared to naturally recruiting eels in the same water body (Stacey et al., 2015) and can carry parasites from one watershed to another (Morrissey & McCarthy, 2008). For these reasons I recommend simply re-opening the streams and allowing the eels to recolonize naturally, which has been very successful in other watersheds. For example, when the Ft. Edward Dam was removed from the Hudson River, eels were observed in upstream habitats that had been inaccessible for 150 years (Hart et al., 2002). Eel abundance also increased significantly after the Embrey Dam in Fredericksburg Virginia was removed in 2004. This dam appeared to have been preventing the migration of smaller individuals and its removal increased eel abundance up to 150 km upstream in less than a year (Welsh & Liller, 2013).

Additional sampling efforts could provide an opportunity for examining eel morphology across watersheds. Despite the panmixia of the American Eel population (all members can breed with all others), phenotypic differences are evident among different areas in the range, or among different habitats types within a specific region (Shepard, 2015b).

For future projects, the study area can be expanded to include the entire range of the Chesapeake Bay. The five longest rivers in the Chesapeake Bay watershed are the Susquehanna, Potomac, Rappahannock, York and James rivers are the five largest rivers in the Chesapeake Bay watershed. The map includes the full extent of the latter three rivers but is missing a large portion of the Potomac River and nearly all of the Susquehanna River, which at 715 km is the longest river on the East Coast that drains into the Atlantic Ocean. This, however, will require additional data from Delaware, Pennsylvania, New York and West Virginia. The dataset also includes fish from the Roanoke and Monongahela Rivers (not shown), which are separate drainages.

By adding additional data layers, future projects may be able to address why some eels move upstream and some do not. For example, the map of streams (Fig. 22) could be updated to include flow regimes and pheromones that could be acting as cues, or eDNA could be used to determine presence/absence in smaller streams that may not have been sampled directly. The methodology in this paper could be used over the entire range of American Eel. For this to be feasible however there must be standardized data collections from each jurisdiction and an effort to combine multiple datasets into a single database. Future studies will also likely need a different method for categorizing land use, since one category (barren land) barely registered. One option is to use a higher resolution raster to further subdivide land use categories. I initially attempted this work with a different raster set that was available online only, but lost access to this resource (and several other datasets) because of the 2019 U.S. government shutdown. This is what drove us to use DEM data from the ASTER archive (a partnership between the United States and Japan) and land cover data from the Université Catholique de Louvain in Belgium.

My recommendation to restore habitat and upstream access is supported by analysis by Kahn (2019). This author used data from the National Marine Fisheries to create an index of relative abundance using annual mean total catch of eels per trip, including eels released by anglers (discards), from the period 1981–2014 combined with commercial landings and the index of relative abundance to estimate the trend in commercial fishing mortality in the form of relative fishing mortality. The findings were that the index declined to 1/7th of the original from 1981 to 1995 but increased from 2003 to 2014, although the 2014 index was only about half of what had been observed in 1981. The American Eel fishery has been stable even while abundance has been increasing. For a species with a commercial fishery to be considered endangered with extinction, it would have to become so uncommon as to be commercially extinct, i.e. that a fishery would be economically unviable to the point that landings would not cover the expenses of fishing. Migrating females are less susceptible to the fishery because silver eels tend to stop feeding and are less likely to enter eel pots (Kahn, 2019).

While there are still nine active silver eel weirs in the Delaware River and tributaries (ASMFC, 2014), all of the others have closed, with the Maine silver eel fishery closing in 2014 (ASMFC, 2013b). Thus, it appears the decline in American Eel is coincident with the construction of dams (which accelerated in the 1950s to 1970s) and the continued presence of these barriers could be the primary reason the population is still at around half of its prior level. Because of the large distribution of American Eel however future studies will need to take into account the entire range to determine the factors affecting carrying capacity.

American Eel can adapt to a variety of habitats through local adaptation and phenotype plasticity. The three life strategies (freshwater, brackish water and marine water) are tied to distinct ecotypes that can be consistently differentiated by polygenic genetic differences and blindly assigned to their habitat of origin, although the mechanism for how this occurs is unclear. Thus, it is necessary to conserve habitat and connectivity across the range to preserve genetic diversity (Pavey et al., 2015). Some of the historical range has already been reduced by the construction of dams for hydropower and water storage. Habitat loss from barriers is considered a historical effect and its population level effects have likely already been realized (Shepard, 2015a).

My conclusions are that some subwatersheds, such as the Potomac and Rappahannock Rivers, of lesser concern, while the areas that merit further study are the York River upstream of Cedar Fork, VA and the James River upstream from Richmond, VA. Both of these watersheds have higher rankings downstream, indicating the high densities of barriers may be affecting upstream eel migration and thus limiting the habitat and carrying capacity of American Eel. Thus, consistent sampling methods and data collection are vital to confirming the results. I recommend implementing standards for eel collection, such as recording the location in decimal degrees, the total length, weight, life stage, sex when applicable presence/absence of parasites, CPUE/CPSE and gear used, in addition to environmental data such as water temperature, salinity, pH and pollutants.

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