AMERICAN EEL BIOLOGICAL SPECIES REPORT

Supplement to: Endangered and Threatened Wildlife and Plants; 12-Month Petition Finding for the American Eel (Anguilla rostrata) Docket Number FWS-HQ-ES-2015-0143

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U.S. Fish and Wildlife Service, Northeast Region

AMERICAN EEL BIOLOGICAL SPECIES REPORT

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This American Eel Biological Species Report has been prepared by the U.S. Fish and Wildlife Service (Service) in support of a Status Review pursuant to the Endangered Species Act, 16 U.S.C. §§ 1531, et seq. This report reviews the best available information, including published literature, reports, unpublished data, and expert opinions. The report addresses current American eel issues in contemporary time frames. The report is not intended to provide definitive statements on the subjects addressed, but rather as a review of the best available information and ongoing investigations. The report includes updates to, and relevant material from, the Service's 2007 American Eel Status Review. The report was published in January 2015 following peer review. The report was revised to correct typographical and minor factual errors and reissued in June 2015.

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EXECUTIVE SUMMARY

This Biological Report (Report) is the supporting material prepared in response to a 2010 petition from the Center for Environmental Science Accuracy and Reliability (CESAR) to the U.S. Fish and Wildlife Service to list American eel (*Anguilla rostrata*) as threatened under the Endangered Species Act, 16 U.S.C. §§ 1531, et seq. This Report supports the 2015 status review for American eel to determine if adding the species to the Federal List of Endangered and Threatened Wildlife is warranted. A previous status review of American eel was conducted in 2007, finding that federal protection under the ESA was not warranted. The 2010 petition from CESAR includes information that became available after the 2007 review—specifically, information regarding marine migrations, panmixia, American eel distribution, climate change, and an exotic parasitic nematode. This Report reviews this information and also updates information in the 2007 review, with respect to American eel biology, distribution, population status, stressors and threats to the species.

American eel evolved more than 2 million years ago, when the ancestral Atlantic eel species gave rise to both the European and American species of eel. As a result of this relatively recent speciation, American and European eel are closely related, have similar genotypes, nearly identical life history characteristics, overlap in their breeding in the Sargasso Sea, and can produce hybrids that are common among eels in Icelandic waters. The abundance of both species has declined in response to similar stressors. Some information on European eel is included here, where it informs the biology of American eel or the assessment of stressors to the species.

American eel undergo several morphological changes from larvae, to glass eel, to juvenile yellow eel, and finally a mature silver eel. The larval and silver eel life stages migrate thousands of miles between marine and continental waters, and are very difficult to study. Larval migration starts as passive entrainment in ocean currents but metamorphosed larvae (i.e., glass eels) are believed to actively swim in order to detrain from these ocean currents and cross the continental shelf. Glass eels do not home to specific estuaries or rivers. Shortly after entering estuaries and rivers, glass eels become pigmented and are often called elvers (i.e., small yellow eels). Yellow eels grow for 2 to more than 30 years before maturing and returning to the Sargasso Sea.

The best available data indicate American eel are a panmictic species—there is a single population that lacks distinct structure, breeds in one location, and shares a common gene pool. The species has phenotypic plasticity that allows eels to adapt to a wide range of habitat types, from estuaries to freshwater headwater habitats. As a result of this plasticity, the species is widely distributed in accessible lakes, rivers, streams, and estuaries from eastern Canada to Venezuela. Despite panmixia, phenotypic differences are evident among different areas in the range, or among different habitats types within a specific region. These differences are due to the survival of individuals with phenotypes that are best

adapted to the local environment. Within larger watersheds, eels that migrate to headwater habitats are more likely to be female, while those that remain in downstream habitats, or in the estuary, are more likely to be male. Females are also more common in the northern portion of the range and in habitats where eel density is low. Males are more common in the southern part of the range and in habitats with high densities of eels. Males tend to grow fast and mature early at small size, while females tend to grow more slowly and mature at much later age and larger size. The life history plasticity that is observed among this diversity of habitats may be an adaptive mechanism that optimizes female growth and egg production while minimizing the investment in male growth.

American eel are distributed throughout most of their historical range, although they are much less abundant than in the past. Commercial harvests of yellow and silver American eels were highest in the 1970s and 1980s, based on landings data that extend back to the 1950s, but those harvests have declined in recent decades. Glass eel harvests continue to be volatile in response to large changes in market prices. Currently, coastwide regulations prohibit the harvest of glass eels except in Maine and a small glass eel fishery in South Carolina. In general, commercial landings may not be reliable indicators of population abundance since they also reflect changing fishery regulations, domestic and foreign market prices, consumer preferences, and decisions by commercial fishers to allocate their effort among various fisheries. For State management purposes, the eel stock is considered depleted—harvests have been reduced and some eel fisheries have been eliminated. Based on glass eel abundance in fisheries, hundreds of millions of glass eels may reach continental waters each year. Based on genetic parameters, spawning eel in the Sargasso Sea may number between 4.7 and 109 million. Although some indices appear to show an increase in eel abundance in recent years, trend analyses do not show a significant change since the 2007 Status Review. The trend in eel abundance is currently considered to be stable.

The effect of passage through hydroelectric turbines was analyzed in the previous status review. Since that analysis was completed, additional upstream eel fishways and downstream bypasses or nighttime turbine shutdowns have improved eel passage at some hydroelectric dams. To the extent that eel passage solutions are effective, they mitigate the effect of multiple dams and turbines within a watershed, or turbines on terminal dams which affect the entire silver eel run from a watershed. Upstream eel fishways can achieve benefits at relatively low cost. Downstream passage facilities, or nighttime shutdowns in lieu of downstream passage facilities, are becoming more common, but are much more costly than upstream eel fishways. Implementing these upstream and downstream passage solutions at dams is crucial to address both access to upstream habitats and passage related mortality, particularly at the lowest dams in the watershed.

The 2007 Status Review did not evaluate climate change stresses to the American eel population because available information at the time was lacking or speculative. Updated information suggests that North Atlantic Ocean habitats are changing in response to

weather, wind, and increasing temperature. These climate changes may affect American eel spawning success, larval growth and survival, or the transport of larvae to continental rearing habitats. Spawning and larval rearing may be particularly vulnerable to climate change since these life stages have specific marine habitat requirements. Larval transport to continental waters may be affected if climate change alters the strength of North Atlantic Ocean currents such as the Gulf Stream. The abundance of elvers entering North American streams and rivers is correlated with changes in the North Atlantic Oscillation, a measure of North Atlantic atmospheric pressure gradient. Although the underlying mechanism is not well understood, this correlation indicates that physical oceanographic processes in the North Atlantic Ocean are linked to the abundance and recruitment of juvenile American eel.

In the last three decades, the exotic parasitic nematode *Anguillicoloides crassus* has become well established in continental waters of the western North Atlantic from Nova Scotia to the eastern United States. It has expanded its distribution within existing watersheds and colonized new watersheds. There is evidence that mean *A. crassus* infection rates have increased over time. Trends in North America mirror the progression of the *A. crassus* infestation about a decade earlier in Europe. The parasite infests the swimbladder and can cause significant eel mortality in crowded aquaculture conditions, but does not appear to cause mortality in natural settings where it may have chronic sub-lethal effects. There is significant speculation about the effect of *A. crassus* on the American eel during silver eel outmigration and spawning, which cannot easily be studied under natural conditions. Some European researchers propose that an eel swimbladder that has been damaged by *A. crassus* interferes with buoyancy control, which may decrease swimming efficiency at sea. To date, it is uncertain whether *A. crassus* impairs the silvering process of American eels, prevents them from completing their spawning migration to the Sargasso Sea, or affects spawning success. Laboratory and/or field research on the swimming ability of infected silver American eels is needed to understand this issue.

This Report concludes that many stressors to the American eel population have not changed significantly since the 2007 Status Review. Some conditions have improved to some degree, such as upstream passage and reduced harvest. Conditions such as downstream passage and the nematode parasite continue to affect the species. Changes in the climate of the North Atlantic Ocean in recent decades may have affected American eel, but the information is too inconclusive to have high confidence that climate change has contributed to the decline of eels.

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1 DISTRIBUTION

Marine and continental waters (estuaries and insular fresh waters) of the western North Atlantic support the American eel (*Anguilla rostrata*, LeSueur, 1817) (Tesch 1977; Avise 2003, pp. 31–33). The distribution of American eel includes accessible river systems and coastal areas having access to the western North Atlantic Ocean and to which oceanic currents regularly transport larval American eels. In the Americas, these drainages and coastal areas span 44 degrees (°) of latitude from 54.3° at Hamilton Inlet, Labrador to 10.3° in northern Trinidad and the north coast of Venezuela (Benchetrit and McCleave 2015, pp. 9–10; Tesch 2003, pp. 92–97; Scott and Crossman 1998, pp. 624–625) (figure 1). American eel are widely distributed throughout this area, including Caribbean Islands, Bermuda, Gulf of Mexico drainages including the extensive Mississippi River watershed, the east coast of the United States and Canada. The native U.S. freshwater range of American eel includes an estimated 29,612 kilometers (km) (18,400 miles (mi)) of coastline, which includes barrier islands and coastline from Maine to Texas (Castiglione 2006, p. 1). Eels may be found far inland to headwaters, although eel density generally decreases with distance inland.

American eel are panmictic—a single spawning population breeds in the Sargasso Sea and their progeny disperse randomly to continental waters of the western North Atlantic (Côté *et al.* 2013, p. 1769, Sullivan *et al.* 2009, pp.1964–1965, see also Section 3). As a result of the oceanic currents that distribute larvae to continental waters, the majority of the American eel population is located along the Atlantic seaboard of the United States and Canada. The distribution of American eel within this extensive continental range is well documented along the Atlantic coasts of the United States, the Saint Lawrence River/Lake Ontario (SLR/LO) watershed and the maritime provinces of Canada. American eel are less common and their distribution is less well documented in the Gulf of Mexico, Mississippi River watershed, and Caribbean Islands. The presence of American eel is least understood in Central and South America, but recent research indicates that American eel may be rare in those watersheds and the southern limit of the distribution is in Trinidad and Venezuela (Benchetrit and McCleave 2015, entire) (figure 1). The status of American eel in each of these areas, including information on commercial landings, is discussed in Section 5.
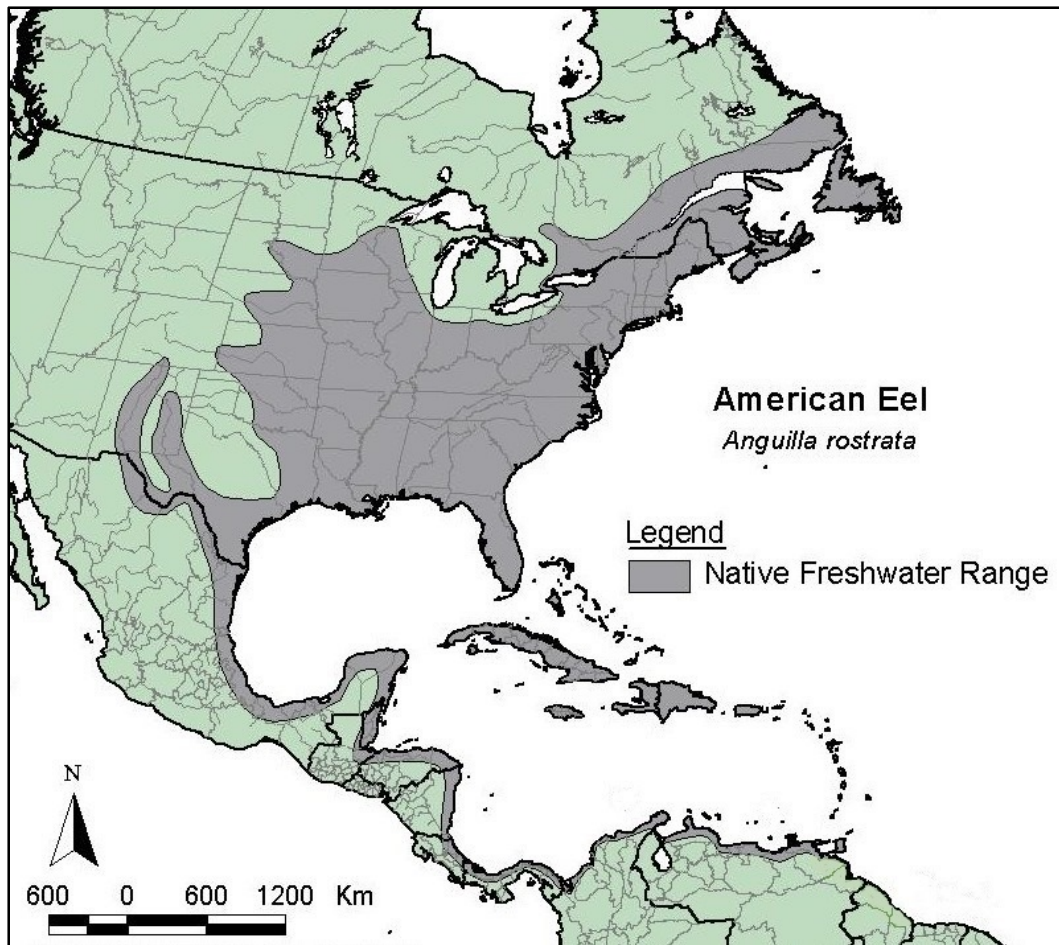
FIGURE 1—Native freshwater range of American eel (*Anguilla rostrata*) in the Americas (updated from NatureServe, 2006).

The American eel was absent from the Great Lakes watersheds of Lakes Erie, Huron, Michigan, and Superior before the completion of the Welland Canal in 1829 (Patch 2006, p. 2). In 1878, the Michigan Fish Commission planted young eels in southern Michigan waters, the Ohio Fish Commission released young eels in the Lake Erie watershed beginning in 1882 (Trautman 1981, pp. 192–193), and eels were stocked in Saskatchewan in 1952 (Scott and Crossman 1998, p. 628).

2 TAXONOMY AND GENETICS

2.1 TAXONOMY

The American eel belongs to the Class Actinopterygii, Order Anguilliformes, Family Anguillidae, and Genus *Anguilla*. Ege (1939, in Lecomte-Finiger 2003, p. 267) described 19 species and subspecies of eel in the genus *Anguilla* based on an extensive examination of morphometric data, such as the number of vertebrae. However, morphometric characteristics have limitations as taxonomic attributes because they overlap in most of the *Anguilla* species. Biochemical characters, such as mitochondrial and microsatellite DNA, are more informative (Aoyama 2003, p. 21).

Contemporary phylogenetic studies of the genus *Anguilla* using genetic markers recognize 16 living *Anguilla* species. Two occur in the North Atlantic, 1 in the North Pacific, 3 in the South Pacific, and 10 in the Indo-Pacific (McCleave 2001a, p. 800; Lecomte-Finiger 2003, p. 275; Watanabe 2003, pp. 14–15). This includes the recently described *A. luzonensis* (Kuroki *et al.* 2012, entire; Watanabe *et al.* 2009, p. 387). The two North Atlantic species, American eel and European eel (*Anguilla anguilla*), are closely related, with the lowest genetic distance among the *Anguilla* species (Tsukamoto and Aoyama, 1998 pp. 140–141; Lecomte-Finiger 2003, p. 274; Watanabe 2003, p. 14). Extensive studies of allozyme variation (i.e., variation among functional proteins such as enzymes) demonstrate that American and European eel share alleles at most of the 15 polymorphic loci that were examined, and measures of genetic similarity are within the range of conspecific populations (Williams and Koehn 1984, in Avise 2003, p. 38; Mank and Avise 2003, p. 310). That is, the two species have diverged so recently that they are closely related and could even interbreed. Contemporary studies using microsatellite methods (variation of non-coding repeating genetic sequences) have confirmed these results (Wirth and Bernatchez 2003, p. 684; Pujolar 2013, p.1762).

The two Atlantic *Anguilla* species are believed to share common ancestry with two Indo-Pacific species, *Anguilla mossambica* and *A. australis* (Tsukamoto and Aoyama, 1998 pp. 141–142). Atlantic eels are distinct from the remaining 11 Indo-Pacific *Anguilla* species, leading to the conclusion that the Atlantic eel species share a common ancestor with *A. mossambica* and *A. australis*. The Atlantic eel lineage diverged from these Indo-Pacific species most likely through the ancient Tethys Sea (Tsukamoto *et al.* 2002, p. 1995, McCleave 2001a, p. 807), although much later dispersal through a tropical Atlantic/Pacific marine connection prior to the closure of the Panama Isthmus cannot be ruled out (Avise 2003, p. 44; Lecomte-Finiger 2003, p. 273).

After becoming isolated in the Atlantic Ocean, American and European eel probably became separate species in the early Pleistocene as a result of the cooling ocean temperature that may have affected the larval migration of the ancestral species (Avise 2003, p. 44).

Mitochondrial DNA studies can provide an evolutionary clock—these studies indicate that the divergence of American and European eel species occurred between 1.9 and 3.8 million years ago (Lecomte-Finiger 2003, p. 273), consistent with early Pleistocene speciation.

From an evolutionary standpoint, the relatively recent divergence of the two Atlantic eel species accounts for not only their similar genotypes, but also their ability to hybridize (Avise *et al*. 1990, p. 1259). Hybrids occur at a very low rate and have been found primarily as yellow eels in Iceland, but also as four glass eels in Europe, and a single larva in the Sargasso Sea (Als *et al*. 2011, pp. 1335, 1339). Albert *et al.*(2006, p. 1903) documented an overall hybrid proportion of 15.5 percent among eels in Iceland, with values ranging from 6.7 percent to 100 percent depending on life stage and location on the island. Hybrids have vertebrae counts and gene frequencies that overlap the ranges common to each species. European/North Atlantic hybrid eels can reproduce and persist beyond the first generation, they occur at a higher rate among yellow eels, and at a higher rate with latitudinal gradient in Icelandic rivers (Albert *et al*. 2006, pp. 1903, 1911; Gagnaire *et al*. 2009, p. 1678). Whether these hybrids are reproductively isolated or comingle with the two Atlantic species is uncertain. Als *et al*. (2011, pp. 1342–1343) suggest that hybrids are the result of rare random crossbreeding in the Sargasso Sea and that larvae show intermediate characteristics. In particular, the authors suggest that hybridization results in a larval phase of intermediate duration, such that larvae metamorphose into glass eels and detrain from ocean currents near Iceland. Hybrids have not been reported from any U.S. or Canadian waters.

2.2 PANMIXIA

Panmixia is defined as random mating of a species within a single well-mixed breeding population. Panmixia among American eel is a matter of the random mating of a mixed population of adults in the Sargasso Sea and the random dispersal of larvae to continental waters. Empirical evidence of panmixia is provided by measures of genetic homogeneity (e.g., a lack of unique alleles). Genetic studies of allozymes, mitochondrial DNA of maternal origin, and microsatellite DNA have all demonstrated that the American eel lacks appreciable phylogeographic population structure (Côté *et al*. 2013, p. 1769; Pujolar 2013, p. 1761; Bernatchez *et al*. 2011, p. 1; Avise 2003, p. 34; Lecomte-Finiger 2003, p. 273; Wirth and Bernatchez 2003, p. 685; Avise *et al*. 1986, p. 4353). Stated more simply, panmixia has been confirmed since studies employing various genetic methods have not found significant genetic variability over the entire range of American eel. In the case of the European eel, the panmixia hypothesis was challenged by evidence for an isolation-by-distance pattern that placed Mediterranean eels in a separate clade (Wirth and Bernatchez 2001, p. 1039). However, this pattern was not replicated with additional data and the inclusion of genetic samples from larvae (Als *et al*. 2011, p. 1333; Pujolar *et al*. 2009, pp. 2039–2040).

The catadromous life history of eels contrasts with anadromous species such as salmon, which also have an oceanic phase but return to their rivers of origin to reproduce in discrete breeding populations that are geographically and/or temporally isolated. Anadromous fishes have adapted to make the best use of the specific habitat characteristics of their home waters and as a result, discrete populations may develop different genotypes over time. In contrast, the panmictic life history strategy of catadromous anguillid eels maximizes adaptability to the changing environments that are encountered by larvae that disperse randomly to many habitat types (Stearns 1977, in Helfman *et al* 1987, p. 52). Thus, American eel lack genetic adaptations to specific habitats, glass eels do not home to specific habitats in continental waters, and eels can rapidly colonize a variety of new habitats or recolonize disturbed habitats (e.g., temporarily blocked, polluted, or overfished) over wide geographic ranges (McDowall 1996, pp. 234–235).

2.3 EFFECTIVE POPULATION SIZE

The effective population size (N_e) is a theoretical measure of the number of individuals in a population who contribute genes to the next generation. Alternatively, N_e may be interpreted as a measure of the genetic "health" of a population, since a larger N_e implies a larger breeding population. However, N_e is not a direct measure of the abundance of breeding adults. Estimates of American eel N_e are discussed here since past decreases in N_e demonstrate the resiliency of the species and the ability to recolonize habitats that have been disturbed.

In a healthy population, N_e is a fraction of the population census size (N_c), although the ratio of N_e to N_c varies among groups of species with different life history characteristics. For example, among marine broadcast spawners such as American eel, N_e may be less than 2,000, and it is generally about four orders of magnitude smaller than N_c (Hauser and Carvalho 2008, pp. 343-345). Based upon estimates of N_e and other population and stock assessment data, Côté *et al*. (2013, p. 1771) suggest that the number of American eel breeders in any given year may be about 50 to 100 million with estimates of 4.7 to 109 million breeding eels from 1997–2008. In an *idealized* breeding population *all* of the reproductively mature individuals contribute equally to the genetic composition of the next generation—that is, N_e equals N_c. For this to be true, Kilman *et al*. (2008, p. 1) state that the idealized breeding population must have the following characteristics:

1. There are equal numbers of males and females, all of whom are able to reproduce.
2. All individuals are equally likely to produce offspring, and the number of offspring that each produces varies no more than expected by chance.
3. Mating is random.
4. The number of breeding individuals is constant from one generation to the next.

Any departure from these characteristics will reduce N_e/N_c and may have negative impacts on the population by increasing genetic drift over time, causing inbreeding depression, decreasing genetic heterozygosity, and possibly fixing rare (potentially maladaptive) genes in the population (Kilman *et al.* 2008, p. 1). These impacts are persistent, since a decrease in N_e diminishes the gene pool for many generations to come. And, panmixia reduces the possibility of the introgression of new genes, since there are no isolated breeding populations where new genes may develop and spread to adjacent populations.

Genetic analyses of N_e can be used to assess past population bottlenecks or founder effects, both of which could result in an N_e estimate that is many orders of magnitude smaller than the extant population. For example, founder effects from the relatively recent origin of the human population result in an N_e on the order of tens of thousands of individuals, despite the fact that N_c is currently well over 6 billion (Kilman *et al.* 2008, p. 1).

American eel N_e is estimated to be about 10,000 using several methods (Côté *et al.* 2013, p. 1771; Wirth and Bernatchez 2003, p. 686; Avise 1988, in Avise 2003 p. 35). Wirth and Bernatchez (2003, p. 686) found a significant, two orders of magnitude decrease in N_e over time and the authors estimated that this demographic decline of American eel occurred between about 9,500 and 62,500 years ago, depending on the population parameters used in their analyses. The authors hypothesize that such a dramatic decline in American eel N_e could have been induced by large-scale events such as a change in the oceanic climate. For example, Wirth and Bernatchez (2003, p. 686) note that the observed decline in American eel N_e corresponds to the most recent glacial maximum during the Wisconsinian glaciation. This glacial maximum affected North Atlantic surface water circulation for more than 1,000 years (see Section 6.1). In summary, the timing of the American eel genetic bottleneck indicates that the population declined significantly in response to climate cooling during the Wisconsinian glaciation but then increased during the Holocene (the current inter-glacial epoch) (Wirth and Bernatchez 2003, p. 686; Lecomte-Finiger 2003, p. 274). It is possible that future climate warming may also impact the ocean habitats used by American eel.

3 LIFE HISTORY

American eel are a facultatively catadromous fish species. Catadromous fishes spawn in the ocean but feed and grow in fresh water or brackish estuaries. This life history strategy provides ample opportunity to study freshwater life stages, but leaves the patterns of marine migration and reproduction uncertain. This section draws upon several references describing the life history of American eel (McCleave 2001a, pp.800–808; Tesch 2003, pp. 1–212; Cairns *et al*. 2005, pp. 3–12; McCleave and Edeline 2009, entire; and 72 FR pp. 4968–4975). American eel are a semelparous species, meaning they spawn only once and then die at sea. American eel reproduce in a nutrient poor, low productivity, mid-ocean gyre. Juvenile rearing and growth takes place in productive continental waters and commonly involves migration between habitats of varying salinity (figure 2).
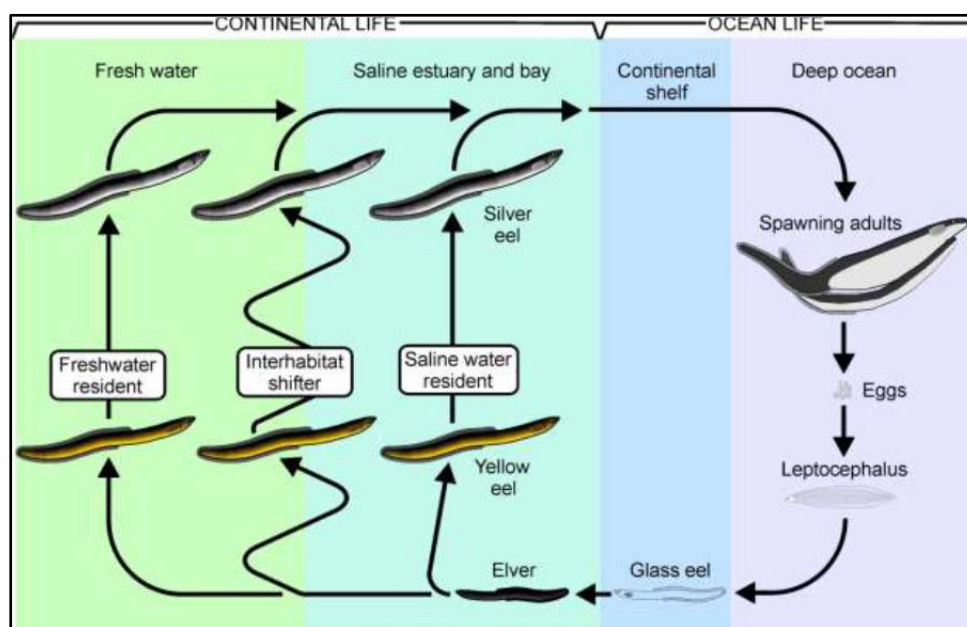
FIGURE 2—Diagram of the American eel life cycle showing ocean life stages and alternative life history patterns of yellow eels during continental life (from Cairns *et al*. 2014, p. 89).

American eel life history provides opportunities for reproduction in a habitat with low predation risk and growth in habitat with abundant food. However, use of these habitats comes with the biological costs of two long migrations. American eel larvae must migrate from ocean breeding habitats to juvenile habitats located in continental waters and mature adults must make the reverse migration. Larval migration is initially accomplished largely by passive drift with ocean currents, but likely requires active swimming to cross continental shelf waters (Miller 2014a entire, Rypina *et al*. 2014, p. 1704). Adult migration requires swimming against, under, or around, these same ocean currents.

American eel, as well as all of the other anguillid eels, are sexually, ecologically, and behaviorally highly adaptive (McCleave 2001a, p. 800). American eel are found in a greater diversity of habitats than any other fishes. The plasticity of the species is related to its adaptability during feeding and growth stages in continental waters (Jessop 2010, p. 341). In contrast to juvenile eel adaptability to a broad range of habitats, successful spawning and larval survival require very specific marine habitat conditions.

3.1 REPRODUCTION

The 16 species of anguillid eels share many life history characteristics. With regard to reproduction, they are all semelparous and they are all believed to spawn in subtropical mid-ocean gyres (Tesch 2003, pp. 98–111). Gyres are the roughly circular patterns of flow that are driven by the Earth's rotation and are typically centered in the large oceans at about 30° from the equator. The North Atlantic Ocean sub-tropical gyre is known as the Sargasso Sea, lying roughly between the West Indies and the Azores (figure 3). Although anguillid eel spawning has never been observed, the timing and location of recently hatched American and European eel larvae were used to estimate the location of their spawning grounds in the southwest part of the Sargasso Sea (Schmidt 1922 p. 194; Kleckner and McCleave 1985, p. 67; Miller and Hanel 2011, p. 5).
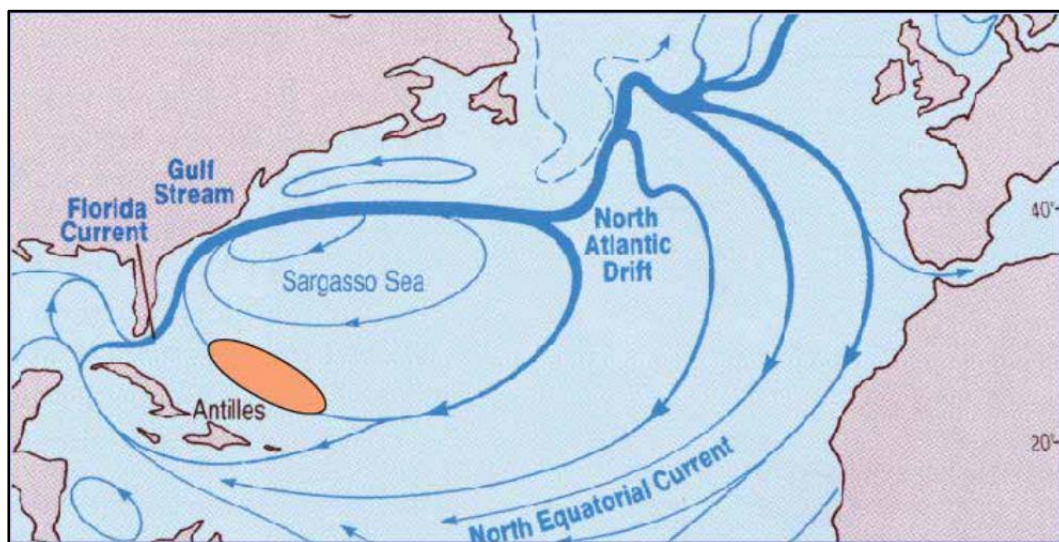
FIGURE 3—Map showing the general pattern of flow in the North Atlantic Ocean Gyre. Ocean currents such as the Gulf Stream, Florida and Antilles currents transport American eel larvae to continental waters. The orange oval indicates the approximate location of the American eel spawning area (from Miller and Hanel 2011, p. 4).

American eel spawn in the southwestern Sargasso Sea (figure 4). This is based upon the distribution of newly hatched American and European eel larvae that have been caught in various plankton trawl surveys in the last 90 years in a region extending from 20° to 29°N and from 52° to 79°W (Als *et al.* 2011, p.1342; Miller and Hanel 2011, p. 5). The European eel spawning zone overlaps to the east in a region that extends from 20° to 30°N and from 48° to 74°W (Als *et al.* 2011, p.1342; Miller and Hanel 2011, p. 5). Trawl data show that there are small differences in peak abundances of American and European eel larvae on a north/south axis, but marked differences in relative dominance of each species on the east/west axis, indicating that, although the general spawning regions of the two species overlap a great deal, American and European eel larvae may have minimal longitudinal overlap in any given year (Munk *et al.* 2010, p. 3598). The distributions of American and European eel larvae also have some temporal overlap, with American eel spawning primarily in February to April and European eel spawning primarily in March to May. This small overlap in time and space results in a low rate of hydribization between American and European eels, as described earlier (see section 2).
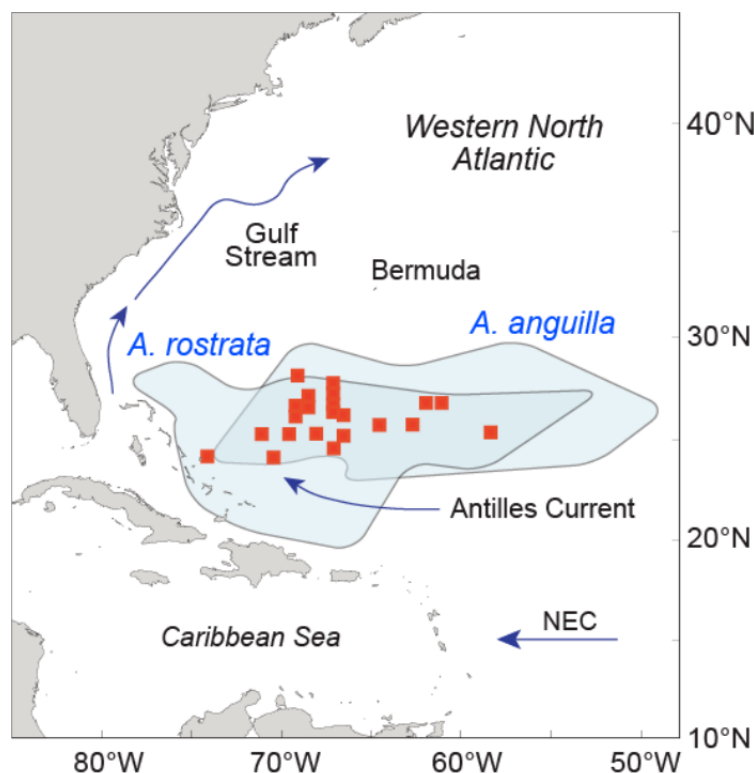
FIGURE 4—Map of the overlapping spawning areas of the two Atlantic eel species (shaded areas), based on the distribution of eel larvae 10 mm long or less. Red squares depict stations where recently hatched larvae (less than or equal to 7 mm) of both species were collected together. Major ocean currents such as the Gulf Stream, Antilles Current and the North Equatorial Current (NEC) are shown (from Miller and Hanel 2011, p. 5).

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Small American eel larvae have been found over a large area of the southwestern Sargasso Sea, although the actual zone of spawning may be much smaller in any particular year. As early as the 1920s, the high temperature, high salinity waters in the southwestern Sargasso Sea were associated with successful eel spawning (Schmidt 1922 p. 206). Thermal fronts, regions of the ocean with abrupt horizontal temperature gradient in surface waters (up to several hundred meters (600 ft)), develop in the Sargasso Sea where northern and southern waters meet in the subtropical convergence zone. It has been hypothesized that these thermal fronts are a cue for migrating adult American and European eels to cease migration and begin spawning (Kleckner *et al.* 1983, p. 289; Kleckner and McCleave 1988, pp. 647–648; Tesch and Wegner 1990 p. 845). Kleckner *et al.* (1983, p. 289) suggest that the American eel likely spawns at depth in water temperatures above 18°C (64°F), where salinity can exceed 36 parts per thousand (ppt). Young larvae less than 10 millimeters (mm) (0.4 inches (in)) long, indicating recent spawning, are found at these thermal fronts and to the south of them, but are not found north of the fronts. Munk *et al.* (2010, p. 3598) have confirmed the relationship between these thermal fronts and the density of both American and European larval eels—the authors also documented the separation of the two species along an east/west gradient with much higher density of European eels located to the east of American eel larvae (figure 5). A northward shift of the 22.5°C isotherm in the Sargasso Sea spawning area was associated with a decline in European glass eel recruitment (Friedland *et al.* 2007, p. 523), possibly by shifting eel spawning northward to areas with unsuitable spawning conditions. A similar correlation has not been documented for American eel.

It is likely that Atlantic eels spawn in the upper 300 meters (m) (~1000 ft) of the water column, based on the temperature and salinity gradients in spawning locations and the presence of early stage neutrally buoyant larvae at those depths (Tesch 2003, p. 89; Greene *et al.* 2009, p. 157). Typical water depths in the spawning area are about 6,000 m (19,700 ft).

3.2 LARVAL DEVELOPMENT AND TRANSPORT

Despite more than 100 years of eel larvae research, a great deal remains uncertain regarding larval eel biology, behavior, and migration. The larval American eel, also known as a leptocephalus (plural, leptocephali), are found in the Sargasso Sea, the Atlantic Ocean, the Caribbean and near-shore waters of the western Atlantic. American eel larvae are unusual in that they have neither scales nor pigmentation, and are filled with a transparent gelatinous energy storage material (Tsukamoto *et al.* 2009 p. 845). It is likely that their transparent body form makes them difficult to find, such that larvae probably experience low predation pressure (Miller 2005, p. 4). Larvae likely have a low metabolic demand and can survive periods of time with little food (Miller 2005, p. 4). Genetic analyses of stomach contents

Sea surface temperature in the western Sargasso Sea in April, 2007 (satellite image, 0.25 °C contours). Dark bands are thermal fronts. Larval eel sampling locations are shown as white circles. Enlargement shows relative abundance of European eel larvae and current velocity vectors at 50 m (164 ft) depth (from Munk *et al.* 2010, p. 3595).
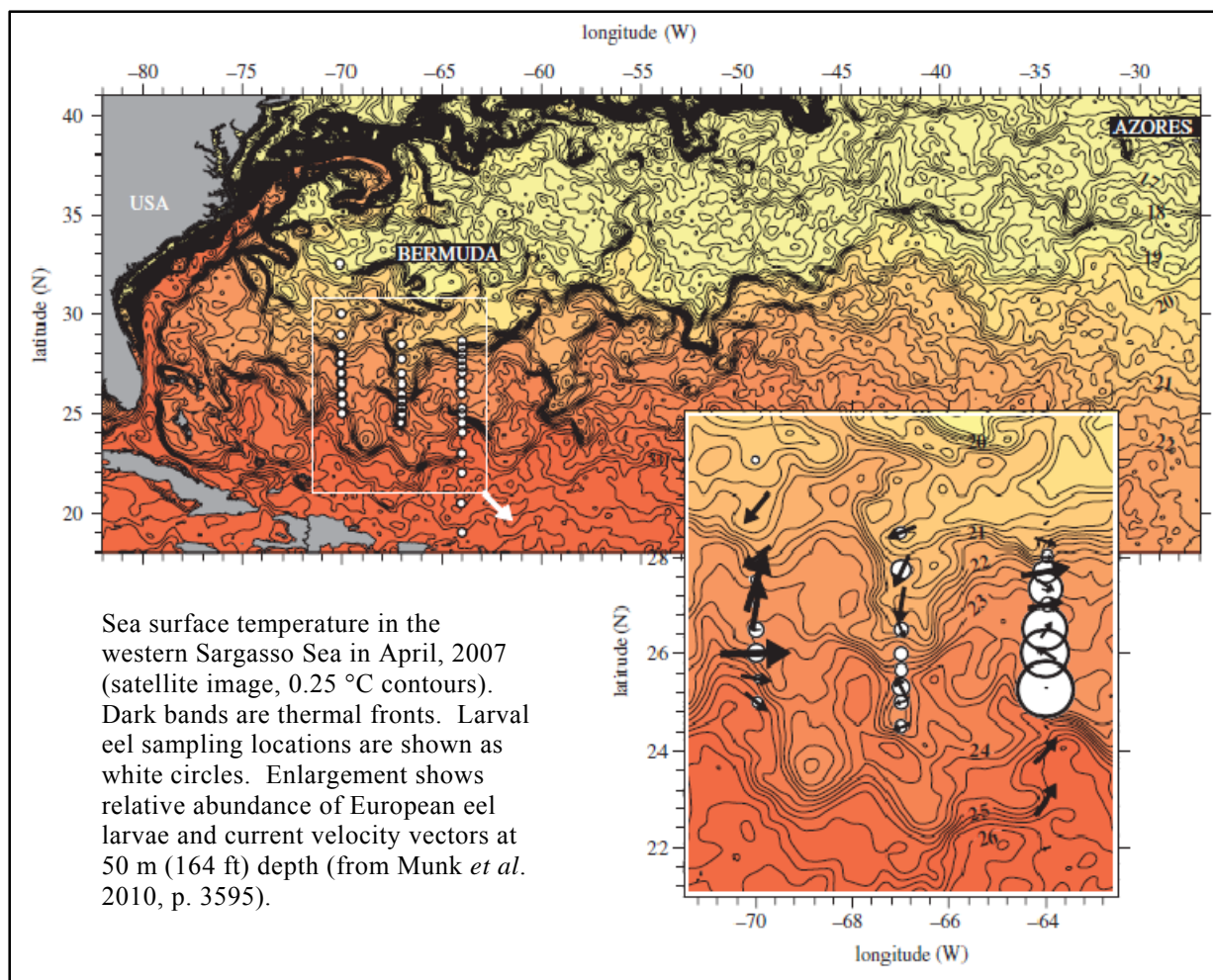
FIGURE 5—Sea surface temperature and larval eel samples collected in the western Sargasso Sea.

have demonstrated that larvae feed on a range of very small plankton taxa, including copepods (Munk *et al.* 2010, p. 3597), although these items may be consumed as detritus rather than live prey. Studies have indicated that larvae feed on marine snow—specific types and sizes of organic detrital particles, such as discarded larvacean houses (a gelatinous case secreted by planktonic tunicates) and zooplankton fecal pellets (Otake *et al.* 1993, pp. 28–32; Mochioka and Iwamizu 1996, p. 447). The survival of small leptocephali also is affected when plankton communities in the photic zone are dominated by cyanobacteria (e.g., *Prochlorococcus* sp.) since they are an unsuitable source of food (Miller 2014b, entire).

Some fish larvae possess the ability to orient in the ocean and "migrate" for small distances (tens of km). However, American eel larvae are initially weak swimmers—orientation and directed swimming has not been observed at the scale that is required to complete the long migration from spawning grounds to continental waters (Kleckner and McCleave 1982, pp. 334–337; Bonhommeau *et al.* 2010, pp. 298–300). After hatching, American eel larvae are

transported by major ocean currents in a generally westward and northward direction to continental waters (Kleckner and McCleave 1985, p. 89). By February through April, American eel larvae up to 40 mm (1.6 in) long are found throughout coastal areas of the mid-Atlantic bight (Able and Fahay 2010, pp. 140–143).

Munk *et al*. (2010, p. 3598) note that although American and European eel spawning areas have a small overlap, American eel larvae are predominantly influenced by westerly currents that entrain larvae north of the Antilles. Most American eel larvae are entrained by the Antilles Current directly from the Sargasso Sea westward into the Florida Current (both currents are components of the Gulf Stream system, see figure 3). The Florida Current transports water from the Caribbean, the Gulf of Mexico, and more distant regions through the Straits of Florida. Some larvae may enter the Florida Current by a more southern route if they are entrained in flows of the Caribbean and then enter the Gulf of Mexico. For example, larvae may be transported on the Caribbean Current through the Yucatan Straights (Kleckner and McCleave 1985, p. 89), to the Gulf Loop Current and then to the Florida Current. These routes likely account for the juvenile American eel that are recruited to Caribbean islands and continental waters of the Gulf of Mexico (Kleckner and McCleave 1982, p. 329–330; Miller 2005, p. 3). The distribution of American eel larvae in the Florida Current was first described by Kleckner and McCleave (1982, pp. 334–337; 1985, pp. 73–77), who noted that these ocean currents deposit larvae to the Continental Shelf of North America at higher densities from Cape Hatteras north to Quebec. Once past Cape Hatteras, the Gulf Stream—which is typically 160 km (100 mi) or greater offshore, but may be as close as 48 km (30 mi) offshore—usually has pronounced meanders. The flow of the Gulf Stream continues to the northeast, mostly paralleling the Atlantic coast and dispersing to become the North Atlantic Drift as it approaches Europe (figure 3) (Miller 2005, pp. 3–4).

American eel leptocephali are generally considered to drift with ocean currents. However, the timing and location of leptocephali indicates that they must swim at critical times to successfully detrain from ocean currents and reach their metamorphosis and recruitment areas (Rypina *et al*. 2014 entire; Miller 2014a, entire). Larvae are distributed in the upper 300 m (~1000 ft) of the ocean currents, where they make diel migrations to the surface at night (presumably to feed) and to deeper waters to avoid predators in daylight (Bonhommeau *et al*. 2010, p. 300). As a result of these diel movements, larvae are subject to transport from complex surface and sub-surface currents. Simulations of American eel larval swimming showed that directional swimming in a random direction improved larval success rates (i.e., reaching continental shelf waters) by more than two orders of magnitude compared to passive drift, and swimming primarily to the northwest further doubled these rates (Rypina *et al*. 2014, p. 1704). Directional swimming resulted in a reasonable distribution of larvae along the shelf break, whereas other movement scenarios left gaps where no larvae reached the shelf, including near the Gulf of Maine where juvenile eels are abundant (Rypina *et al*. 2014, p. 1704). Active directional swimming yields transit times of

about one year, and reproduces observed larval/glass eel observations (Rypina *et al*. 2014, p. 1704). Active directional swimming seems to be the only way American eel leptocephali can cross the Gulf Stream to reach coastal waters.

3.3   METAMORPHOSIS AND RIVER ENTRY

American eel undergo a dramatic metamorphosis from leptocephalus larva to "glass" eel, a life stage that lasts only a few months, bridging the gap between larva and "elver" (a young yellow eel) (figure 2). (Note: a first year elver is referred to as young of the year or YOY.) Metamorphosis from larvae to glass eel occurs from about 6 to 12 months post-hatch (Kleckner and McCleave 1985, p. 78), usually in the fall/winter months of October to March. The environmental cues and/or biological triggers of metamorphosis are unknown, but the distance that larvae are transported to southern versus northern portions of the range differs significantly, which suggests that the timing of metamorphosis determines where a particular larval eel will arrive in continental waters (Miller 2005, p. 2; Pratt *et al*. 2014, p. 3). That is, larvae that metamorphose early will recruit to lower latitudes than those that metamorphose later.

As they metamorphose, the laterally compressed leaf-like shape of the leptocephalus transforms into a small, elongate, transparent, characteristically eel like fish, with the full complement of fins found on an adult eel. This transformation results in a decrease in body length and weight due to the loss of tissue water and an increase in body thickness (Fahay 1978 <u>in</u> Atlantic States Marine Fisheries Commission (ASMFC) 2012, p. 8). Miller (2005, p. 2) proposes that the metamorphosis from leptocephalus larva to glass eel makes possible the directional swimming ability that is needed to detrain from the Gulf Stream system and cross Continental Shelf waters, since eel larvae do not have this swimming capability. Glass eels arrive in coastal waters earlier in southern portions of the range, and at smaller size, compared to the later arrival of larger glass eels in the north (table 1, figure 6) (Pratt *et al*. 2014, p. 3; ASMFC 2012, p. 6–7). Glass eels require 60–110 days to swim from the Gulf Stream to the coast of New Jersey or North Carolina (Wuenschel and Able 2008, p. 779; Powles and Wharlen 2002, p. 302). Within a few days of taking up residence in brackish or fresh water, the glass eel transforms to a pigmented elver. Elvers typically weigh much less than 1 gram (0.03 ounces), are capable of surviving the osmotic challenge of entering fresh water, and generally still retain a strong migration urge, although they are now driven to move upstream rather than across the continental shelf.

Glass eels and elvers can arrive in great density, but with significant seasonal and yearly variation in recruitment (International Council for the Exploration of the Sea (ICES) 2001, p. 2). For example, in the 9 years of records collected between the years 1982 to 1999, estimated recruitment to the Petite rivière del la Trinité, Quebec varied roughly four-fold, from a low of 14,014 elvers to a high of 61,308 (ICES 2001, p. 36). Glass eels and elvers have been collected in North Carolina from two sites in the Beaufort Inlet estuary for 18

TABLE 1—Timing and average length reported for glass-stage American eel upstream migrants in various locations (from ASMFC 2012, p. 131).

Location	Migration Timing	Average Length (mm)	Reference (from ASMFC 2012)
N. Gulf of St. Lawrence	Jun–Aug	62	Dutil et al. 1989
Nova Scotia (various)	Apr–Jun	59.5–64.8	Jessop 1998
Nova Scotia	May–Jul	60.3	Jessop 2003
East R., Nova Scotia	May	60	Wang and Tzeng 2000
Musquash R., New Bruns.	April	60	Wang and Tzeng 2000
Annaquatucket R., RI	Apr–May	58	Haro and Krueger 1988
Annaquatucket R., RI	April	59	Wang and Tzeng 2000
Gilbert Stuart Brook, RI	May	58	Sorenson & Bianchini 1986
Little Egg Inlet, NJ	Jan–Jun	48.7–68.1	Wuenschel and Able 2008
Indian R., DE	Jan–Apr	57	Clark 2009
North Carolina	March	48	Wang and Tzeng 2000
Beaufort, NC	Feb–Mar	53.6	Powles and Warlen 2002
Roanoke River, NC	Feb–Mar	57.7	Overton and Rulifson 2009
Altamaha R., GA	late winter	52	Helfman et al. 1984b
Florida	Jan–Feb	49	Wang and Tzeng 2000
Haiti	Dec	48	Wang and Tzeng 2000
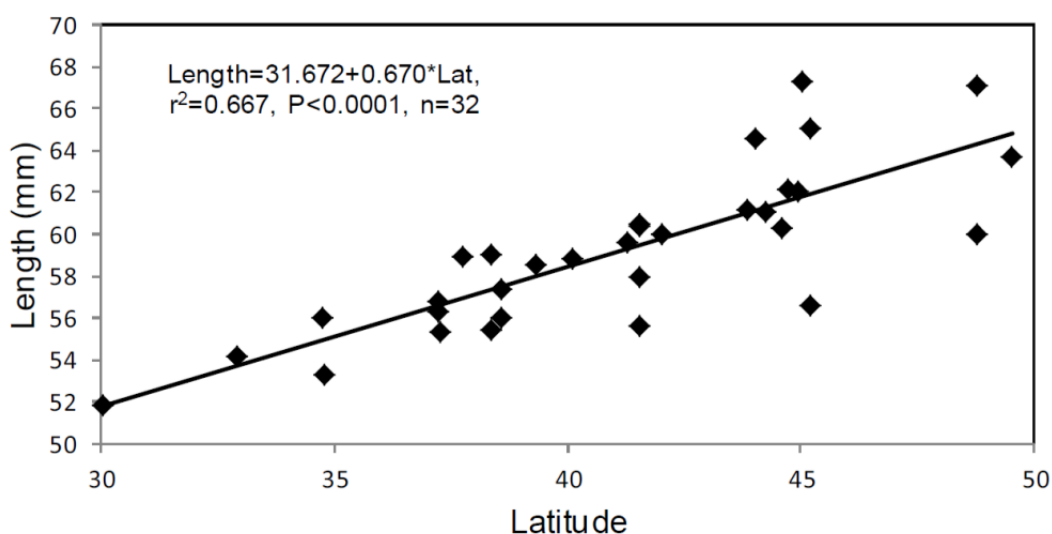
FIGURE 6—Mean length of glass eels at various latitudes (from Cairns *et al.* 2014, p. 133).

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years. Densities have varied from 1.5 to 14.0 eels/100 cubic meters (m^3) (3531 cubic feet (ft^3)) (Powles and Warlen 2002, p. 301). Annual glass eel densities in Beaufort Inlet were only weakly correlated with densities in the Little Egg inlet in New Jersey (Sullivan *et al.* 2006, p. 1087). The authors found weak correlations between glass eel density and several environmental parameters (water temperature, moon phase, and neap tide), and a strong correlation with winter precipitation (Sullivan *et al.* 2006, pp. 1089–1091).

Glass eels and elvers use selective tidal stream transport for migrating upriver (Sheldon and McCleave 1985, p. 425). In the St. Lawrence Estuary, glass eels are able to travel upstream at the rate of 10 to 15 km/day (6 to 9 mi/day) (Dutil *et al.* 2009, p. 1980), but the speed of elvers is reduced to an average of 1 to 2 km/day (0.6 to 1.2 mi/day) further up the St. Lawrence River (Verdon and Desrochers 2003, p. 139). Elver migration typically occurs at night and is related to moon phase, increased river discharge, and reaching a minimum water temperature threshold of 10 to 12°C (50 to 54°F) (Martin 1995, p. 898; Jessop 2003 p. 31; Schmidt *et al.* 2009 p. 718; Sullivan *et al.* 2009 p. 1949).

3.4 YELLOW EELS

Yellow eels are able to adapt and exploit almost all aquatic habitats, from estuaries or full salinity marine habitats, to lakes and rivers where they may live to more than 30 years before maturing into silver eels and migrating to the sea to spawn (Helfman *et al.* 1987, pp. 44, 50; McCleave and Edeline 2009, entire) (see figure 2 for life stage illustrations). Yellow eel dispersal in these different types of habitats determines important life history and demographic traits such as growth rate, sex differentiation, age/size at maturity, and, ultimately, the spawning escapement and biomass produced in a given watershed (Jessop *et al.* 2002, pp. 217–218; Morrison *et al.* 2003, pp. 90–92; Thibault *et al.* 2005, p. 36; Lamson *et al.* 2006, p. 1567; Daverat *et al.* 2006, p. 2; McCleave and Edeline 2009, p. 97). Estuaries provide abundant food and result in the highest yellow eel growth rate (Fenske *et al.* 2010, p. 1707) (see also section 4.2.1). Yellow eel life history patterns have been identified in relation to migration and foraging movements among marine, estuary and freshwater habitats (Feunteun *et al.* 2003, p. 201; McCleave and Edeline 2009, p. 99–102; Hedger *et al.* 2010, p. 1294). In fresh waters, home-range dwellers may stay within a discrete home range for long periods of time, while nomads and pioneers may relocate in response to competition with other eels or changes in habitat suitability (Oliveira 1997, p. 638; Lamothe *et al.* 2000, p. 398). These behaviors represent different life strategies towards reaching a minimal threshold for maturation.

Upstream movements are often to lakes, ponds, and upstream river reaches where there may be fewer yellow eels, less competition, and greater opportunity for eel growth. Lamson *et al.* (2006, p. 1572) traced yellow eel movements in Prince Edward Island, Canada using otolith (i.e., ear bone) microchemistry and found that 69 percent of individuals moved between salt and fresh water, and some eels completed their life cycle entirely in brackish

water habitats. Other research (Thibault *et al*. 2007) indicates that movements between fresh water and estuarine zones may be regular and seasonal in nature, as a response to low winter temperatures in the estuary. Eels that move upstream tend to be females, although it is not known if eels that are destined to become female are predisposed to migrate upstream, or if the characteristics of upstream habitats cause young eels to become female. Yellow eels in upstream reaches of rivers and inland lakes tend to be older, larger, females—males are extremely rare in these habitats (Helfman *et al*. 1987, pp. 49–50; Oliveira 1999, pp. 799–800). Sexual differentiation, as it relates to habitat use and life history development, is discussed in section 3.5.

Yellow eels may abandon their home range and make long movements, particularly to upstream habitats. Yellow eel upstream movement occurs from dusk to dawn (Verdon *et al*. 2003, p. 133) in the all months of the year with peak movement dependent on temperature and latitude (Richkus and Whalen 2000, p. 83). For example, yellow eels in the Richelieu River, Quebec, which is the outlet of Lake Champlain, were caught in the fishway at Chambly Dam in all months of operation from June through October (Verdon *et al*. 2003, p. 133). Yellow eels reach the Moses-Saunders Power Dam (the second dam on the St. Lawrence River) and pass one of two fishways in July, with a secondary peak in early October (McGrath *et al*. 2003b, pp. 162–163). However, these eels migrate about 300 km (186 mi) from the estuary to reach the Moses-Saunders Dam, and they are generally 5 to 7 years old when they pass the fishways at the dam although much older eels (11 to 12 years) were typical during the period of lowest abundance in the 1990's to 2003 (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2012, p. 38). The October peak in upstream movement may be unique to older upstream migrant eels, or to this site.

Fishways have been designed and built specifically for the passage of elvers and yellow eels (Haro 2013, entire). They typically consist of a sloped ramp with some type of peg or roughened substrate. Transport and attraction water may be provided by gravity or with pumps. Eels will pass Denil (Baras *et al*. 1994, p. 7), steeppass, vertical slot, and Ice Harbor type fishways (Alex Haro, USGS, unpublished data), but usually do so only at larger sizes. Conventional fish lifts are typically ineffective for small eels, which usually pass through retention screens upstream of lift hoppers and are not lifted in large numbers. They can also be attracted into and trapped within the attraction water systems of fish lifts.

The size and age composition of upstream migrating yellow eels can be different at the first dam compared to subsequent dams. For example, upstream movement has been monitored at numerous Maine dams for more than a decade. Peak upstream movement at the initial dam is typically in early June and consists mostly of YOY (figure 7). At dams located further upstream in Maine watersheds, movement occurs later in the season and multiple sizes and age classes are common—at the second, fourth, and fifth dams on the mainstem
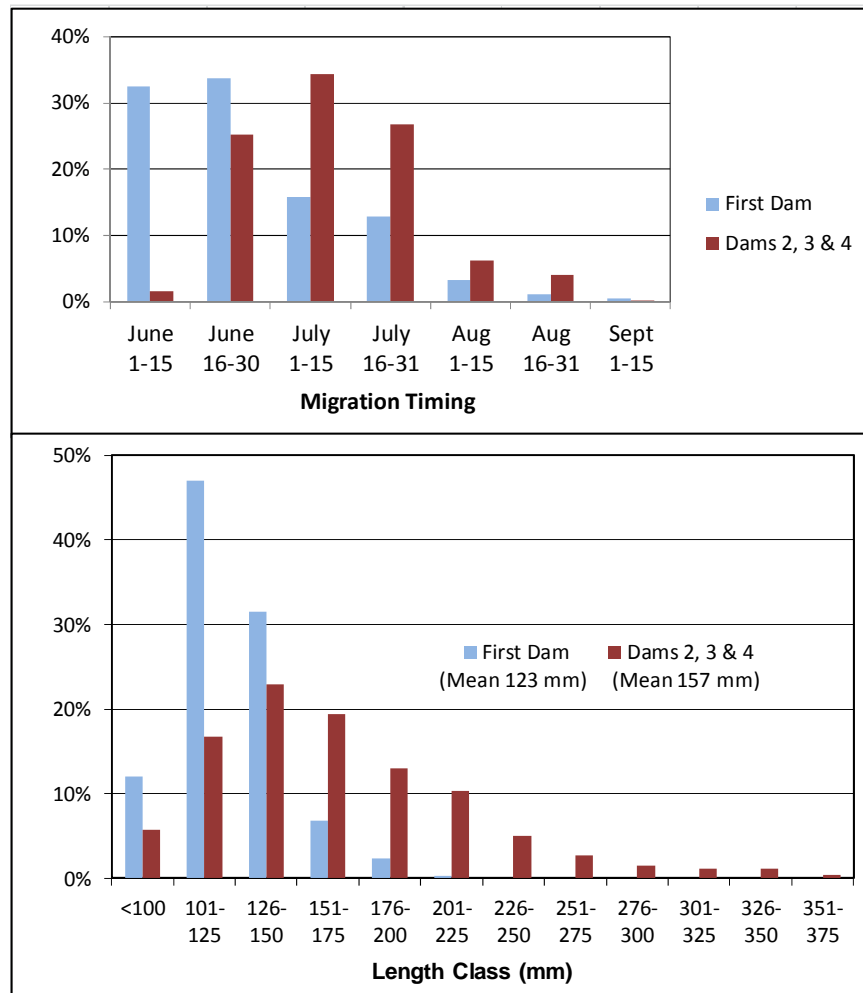
FIGURE 7—American eel upstream migration timing (upper panel) and size distribution (lower panel) at the first dam compared to a composite of dams two, three and four. Data for the first dam are mean bimonthly fishway trap catches (1998 to 2013, G. Wippelhauser, MDMR, unpublished data), and 2012 size distribution at the Benton Falls eel fishway, Sebasticook River, Maine (MDMR 2013, p. 7). Data for subsequent dams are 2009 to 2010 pooled data from eel fishways at the Orono, Milford and West Enfield dams on the Penobscot River, Maine (ASA 2010, pp. 7–8; ASA 2011, pp. 5–6).

of the Penobscot River, Maine, eels moved upstream from mid-May through early September with peak passage in late June and July (figure 7) (Aquatic Science Associates (ASA) 2010, pp. 7–8; ASA 2011, pp. 5–6). On average, 87 percent of the upstream migrating eels passed these sites between June 16 and July 31. The onset of yellow eel upstream movement at these Penobscot River fishways appears to be triggered by a threshold water temperature of 18°C, but is inhibited by high flows that occur earlier in the season and may interfere with finding the fishway entrance.

The upstream migrations of yellow eels through eel fishways on mid-Atlantic rivers extend over longer periods of time than in northern portions of the range, probably in response to the longer period of suitable water temperature. Welsh and Liller (2013, pp. 486–489) documented that upstream eel movement at a fishway on the Shenandoah River occurs from May to September at water temperatures above 18°C. Peak passage events were primarily in response to freshets—in 2004, 54 percent of the eels passed the fishway during 2 days of hurricane-related high flows. A second hurricane triggered upstream movement that included 33 large eels (500 to 731 mm (20 to 29 in)), although it is uncommon for large eels to use eel fishways (Welsh and Liller 2013, pp. 485, 488–489). Hammond and Welsh (2009, pp. 318–320), conducted a study of telemetered eels in the Shenandoah River reach downstream of the fishway described above and documented upstream movement in spring, downstream movement in fall, increased movement in response to higher flow, and nocturnal movement with no consistent response to night light levels.

Information on mortality rates of yellow eels is limited. Initially, elvers may experience high mortality rates during the transition from saltwater to fresh water as a result of low pH, high initial density, or predation by resident eels and other fishes (Jessop 2000, p. 514). Vøllestad and Jonsson's (1988 in Jessop 2000, p. 523) research indicates that eel mortality in fresh water is density dependent when elver numbers exceed a certain abundance. Although it is not certain if early juvenile mortality is high throughout the range of the species, this supports the observation that oceanic conditions may deliver relatively high quantities of elvers to rivers (Jessop 1998 in Jessop 2000, p. 523), to the point that carrying capacity of the freshwater habitat may be exceeded (Jessop 2000, p. 523). Mortality rates likely decrease with size. One study in Prince Edward Island, Canada, calculated loss from the population due to mortality and emigration. Estimates of loss in American eel yellow eels from the Prince Edward Island study are reported at 22 percent, with mortality rates decreasing to 12 to 15 percent as the juvenile yellow eels age (Anonymous 2001 in Morrison and Secor 2003, p. 1498), likely due to lower mortality from predation and starvation as size increases.

The enormous dietary breadth of eels reflects their great adaptability with respect to nearly all conditions of water bodies. Yellow eels are opportunistic feeders, consuming nearly any live prey that can be captured. Smaller eels eat benthic invertebrates; larger eels include mussels, fish, and even other eels in their diets. Yellow eels also adapt to seasonal changes, decreasing intake or ceasing to eat during the winter. Eels can also respond to local abundances of appropriately sized prey through the seasons (Tesch 2003, pp. 152–163). This adaptable diet allows for resource partitioning as well as the ability to withstand changes in local environmental conditions and the ability to occupy a geographically wide variety of habitats.

3.5 SEXUAL DIFFERENTIATION

Prior to sexual differentiation, American eels are intersexual, meaning they have no morphologically differentiated sex chromosomes and can develop into either sex (McCleave 2001a, p. 803). It is only when yellow eels reach a length of about 200 to 350 mm (about 10 to 14 in) that it is possible to distinguish males from females histologically. According to Davey and Jellyman (2005, p. 37), "Male fitness is maximized by maturing at the smallest size that allows a successful spawning migration (a time-minimizing strategy) whereas females adopt a more flexible size-maximizing strategy that trades off pre-reproductive mortality against fecundity…gender is determined principally by environmental factors." Specifically, American eel gender is related to habitat characteristics such as the relative proportions of lake versus stream habitat, latitude, salinity, and productivity (Côté *et al*. 2009, pp. 1941–1944), and to demographic attributes such as eel density, growth rate, age at maturity, length and weight (Oliveira and McCleave 2000, p. 141; Fenske *et al*. 2010, p.1699). In response to these habitat and demographic attributes, it is common for water bodies to have highly skewed sex ratios among eels with developed gonads (Helfman *et al*. 1987, p. 46; Oliveira *et al*. 2001, p. 947). Studies indicate that increased density of eels in a particular area increases the proportion of male eels, while lower density favors more females (Tesch 2003, pp. 43–46). High eel density resulted in 90 percent male silver eels in a Rhode Island stream (Krueger and Oliveira 1999, p. 383) and produced 98 percent male silver eels in a Maine River (Oliveira *et al*. 2001, p. 943).

At the northern extreme of the range in Quebec and Newfoundland, 99 percent of differentiated yellow eels were female (Krueger and Oliveira 1999, pp. 384–385). Female size at migration is also positively correlated with latitude—in Canada, female silver eels often exceed one meter (39 in) in length (Oliveira 1999, p. 797). In contrast, female silver eels from rivers in the southeast United States are typically 450 to 600 mm (18 to 24 in) (table 2). Male length is not correlated with latitude and most males tend to mature and begin migrating at about 400 mm (16 in), regardless of habitat characteristics or latitude (Oliveira 1999, p. 797).

Female age was not related to latitude, but male age showed a positive correlation (Oliveira 1999, p. 795). Growth rates for both females and males were inversely related to latitude, with slower growth at higher latitude (Oliveira 1999, p. 795), presumably due to lower temperatures and shorter growing seasons at higher latitudes.

TABLE 2—Average length, age, and timing of migrating silver-phase American eels by location and sex. Length and age ranges are in parentheses. (From ASMFC 2012, p. 132)

Location	Migration Timing	Female		Male	
		Len. (mm)	Age (yrs)	Len. (mm)	Age (yrs)
St. Lawrence River (Upper)	Jun–Oct	957 (890–1,123)	20, 21	NA	NA
St. Lawrence River	Aug–Nov	853 (475–1,000)	13, 14	NA	NA
St. Lawrence Estuary	Aug–Nov	847 (526–1,219)	20–23	NA	NA
Newfoundland	Aug–Sept	684 (431–931)	13 (3–32)	340 (329–361)	(4–15)
New Brunswick	July–Oct	491 (284–733)	NA	317, 326	NA
Nova Scotia	Aug–Nov	551 (394–945)	19 (8–43)	392 (346–473)	12.7 (6–18)
Maine	Aug–Oct	(502–538)	16 (6–18)	(344–359)	12 to 13
SE Cape Cod	Nov	642	NA	373	NA
Rhode Island	Sept–Dec	506 (410–867)	12.8 (6–20)	(228–400)	10.9 (4–15)
Connecticut River	Sept–Oct	707	NA	NA	NA
Indian R., Delaware	Aug–Nov	571 (367–774)	12 (7–20)	330 (264–412)	7.4 (4–16)
Assateague Is., MD	Dec	636 (609–658)	NA	NA	NA
Chesapeake Bay, MD	Oct	NA	NA	306 (275–360)	5.1 (3–10)
Chesapeake Bay, VA	Nov	(366–452)	NA	(395–438)	NA
SE of Chesapeake Bay	Dec	551 (512–579)	NA	NA	NA
Cape Charles, Virginia	Nov	633 (418–845)	NA	372 (339–438)	NA
Potomac R., Virginia	NA	(600–800)	(5–11)	350	NA
Shenandoah River, West Virginia	Sep–Dec	871 (560–1,118)	(10–19)	NA	NA
Cooper River, South Carolina	NA	594 (369–834)	6, 7.6	288 (214–322)	3
Charleston Harbor, South Carolina	NA	550	5.8	317	2.7
Altamaha R., Georgia	Oct–Mar	586 (413–682)	6.8 (4–13)	329 (282–411)	4.8 (3–10)

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The plasticity of American eel life history and demographics results in spatially varying selection from a common gene pool—that is, habitat characteristics can affect the expression of gene complexes and resultant phenotypes (Côté *et al*. 2015, pp. 251–255; Gagnaire *et al*. 2012, p. 731). Although poorly understood in anguillid eels, spatially varying selection may occur among larvae, glass eels, yellow eels, or silver eels in response to the demographic and habitat attributes described above. For example, glass eels translocated from the maritime provinces of Canada to the Upper St. Lawrence River basin matured earlier and with a higher proportion of males than resident wild eels. Bernatchez (2014, entire) attributed this result to selection for certain phenotypes soon after arriving in fresh water. Verreault (2014, entire) monitored the Richelieu River silver eel migration and found that migrants that originated from translocated glass eels were about 300 mm (12 in) smaller at maturity than their naturally recruited counterparts. He also found that they matured by about eight years old, as opposed to about age twenty among naturally recruited eels. Translocated eels also showed about a twenty day migration delay reaching the estuary, only 500 km (311 mi) from stocking location, which may have implications for reproduction synchrony in the Sargasso, 3500 km (2175 mi) further.

Balk and Oliveira (2014, entire) studied female reproductive life history traits (age, total length, body composition, energy density, and parental investment in eggs) of silver eels from rivers in Massachusetts, Nova Scotia and the St. Lawrence River (both translocated and natural). Although age, total length, and total energy were greater in naturally occurring St. Lawrence River eels, the energy *density* was greatest in the stocked eels. Parental energy investment in the eggs was similar for all eels. Age and length of translocated eels from the St. Lawrence River were similar to eels from Nova Scotia and Massachusetts locations and to other locations in the species range with similar habitat conditions. Balk and Oliveira (2014, entire) hypothesized that transplanting eels to the upper St. Lawrence River system creates localized habitats that are similar to densely populated coastal river systems and the resulting female traits are consistent with this scenario. That is, selection for males in the St. Lawrence River translocation experiment took place in response to higher eel densities several years following translocation, rather than prior to translocation.

In summary, it appears that the interaction of eel density, habitat productivity, and growth rate determines the sex of an eel and its age at maturity. However, it is unclear whether habitat characteristics drive biology, or whether eels destined to become a certain sex select the appropriate habitat for that life history. Eels that occupy productive habitats, particularly estuaries with high densities of eels, mostly mature as males while those in headwater habitats and northern latitudes grow more slowly and mature as large fecund females. It has been postulated by Krueger and Oliveira (1999, p. 381) that this environmental sex determination is adaptive, resulting in vast numbers of small males in productive coastal habitats, relatively close to the spawning area, allowing much larger and

more fecund females to occupy most of the available eel habitat. Knights *et al.* (2006, p. 13) argue that this life history strategy also is adaptive in conditions of declining recruitment—that is, when recruitment declines so will overall density and the tendency to migrate far upstream. This increases individual scope for growth in productive waters closer to the ocean and leads to a relative increase in the number of females—to wit, a mechanism that compensates for lower abundance with increased fecundity. These compensatory mechanisms may take several generations and many years to manifest, but it confers enormous benefits in the face of stressors, past, present and future, such as glaciation, tectonic events, climate warming, and changes in ocean currents (Knights *et al.* 2006, p. 13).

3.6 MATURATION AND SILVERING

American eel spawning migrations begin with a sexual maturation process known as "silvering," a biological transformation that is required for seaward migration and reproduction. Silvering marks the end of the growth phase and the development of gonads. Silvering prepares the adult eel for migration in a fully marine environment. Unlike the predictable smoltification process that prepares juvenile salmon for a marine migration, silvering of eels is largely unpredictable. Silvering begins at ages from 3 years to more than 30 years, with the females silvering at later ages and the mean age increasing with latitude—for example, silvering in the Chesapeake Bay region occurs at ages from 6 to 16 years (Helfman *et al.* 1987, pp. 44–45) but at 8 to 23 years in Canada (Cairns *et al.* 2005, p. 11). Silvering transforms eels from a bottom oriented somewhat sedentary yellow eel to a silver eel that is adapted for prolonged oceanic migration and reproduction (van den Thillart *et al.* 2005, p. 12). The silvering process is completed during the marine migration when gonads become fully mature. While still in fresh water, eels may reverse the onset of silvering and revert to the yellow eel life stage (Fontaine *et al.* 1982, Dollerup and Graver 1985, <u>in</u> van den Thillart *et al.* 2005, p. 56).

Environmental factors may play a role in the triggering of silvering. Habitat conditions, such as food availability and temperature, will influence the size and age of silvering eels, as described previously. Thus, variation in length and age at maturity can occur in different habitats (e.g., freshwater habitat versus estuarine habitat), within a restricted geographic range, as well as over larger geographic scales. Temperature and length of the growing season are negatively correlated with latitude, and thus, age at maturity is strongly correlated with latitude (McCleave 2001a, p. 803). Characteristics of female silver eels vary across the species' range. Eels from the St. Lawrence River and Lake Ontario, where migration distances are great, show slower growth and greater length, weight, and age at migration, preparing them, it could be assumed, for the longer migration. In contrast, eels from the southeast have a shorter migration and migrate at smaller size and later in the year.

Van den Thillart *et al.* (2005, p. 56) reviewed European eel silvering and the conditions that promote silvering. Silvering in American eel is very likely similar to the process in the closely related European eel. The authors determined that more than anything else, optimal growth conditions accelerate silvering. This has been observed in aquaculture, under experimental conditions, in brackish water, and at low latitudes. For example, Morrison *et al.* (2003, p. 95–96) found annual growth rates of eels in brackish water were two times higher than growth rates of eels that resided entirely in fresh water. Also American eels in U.S. southern Atlantic coast waters develop into silver eels about 5 years sooner than northern populations (Hansen and Eversole 1984, p. 747; Helfman *et al.* 1984, p. 139), likely as a result of warmer water which accelerates growth and extends the growing season (Helfman *et al.* 1984, p. 138).

Variation in maturation age benefits the population by allowing different individuals of a given year class to reproduce over a period of many years, which increases the chances of encountering environmental conditions favorable to spawning success and offspring survival. For example, variability in the maturation age of eels hatched in 2015 may result in spawners throughout 2020 to 2040, during which time favorable environmental conditions are likely to be encountered in some years.

Male and female eels appear to need to reach a certain size to begin the silvering process, with this size increasing with age. Thus, rapidly growing eels will silver at smaller sizes than slow growing eels. In males, silvering happens at a very early stage, at a typical size of about 350 to 400 mm (14 to 16 in). In females, silvering happens at a size greater than 400 mm (16 in) and may exceed 1 meter (39 in), depending on latitude (Goodwin and Angermeier 2003, p. 530; van den Thillart *et al.* 2005, pp. 31, 55).

Silvering is a gradual process that appears to be initiated by a peak in growth hormone in late spring (van den Thillart *et al.* 2005, p. 60). By late summer, eels metamorphose in preparation for migrating back to the spawning grounds. They have a silvery body color, enlarged eyes and nostrils, and a more visible lateral line (Dave *et al.* 1974; Lewander *et al.* 1974; Pankhurst 1983; and Barni *et al.* 1985 <u>in</u> van den Thillart 2005, p. 12). There is also enlargement of eye diameter with rods predominating over cones in the retina, and retinal pigments blue-shifted (Pankhurst 1983). In preparation for sustained swimming, there is an increase in fat content, increased red muscle mass, and increase in muscle performance (Ellerby *et al.* 2001, p. 1369). Immature egg diameter (Dutil *et al.* 1985, p. 455) and the gonad mass to body mass ratio (McGrath *et al.* 2003a, p. 315) both increase. As the structure and metabolism of the liver changes, the swim bladder also changes, allowing for increased gas deposition rates and decreased loss of gas (McCleave 2001a, p. 804). Swim bladder gas deposition rates of silver eels increased three to five times greater than similar sized yellow eels, and were presumed to increase further as maturation is completed during the marine migration (Kleckner 1980, p. 1481).

A drop in temperature appears to trigger the final events of metamorphosis (gut regression and cessation of feeding), which will lead to migratory movements under the appropriate environmental conditions. It is theorized that responding to a drop in temperature would help to synchronize outmigrating eels, thus increasing their chances of reaching the Sargasso Sea simultaneously. Conversely, increasing temperatures, delays in migration, or possibly low fat content will cause eels to start feeding again and to revert to a yellow resident stage. It has been observed that even after eggs and sperm have developed, eels are capable of gut regeneration and feeding (Fontaine *et al*. 1982, Dollerup and Graver 1985, <u>in</u> van den Thillart *et al*. 2005, p. 56). The conditions encountered during oceanic migration, such as the high pressure eels experience at depth in the open ocean, may complete sexual maturation (Fontaine *et al*. 1985 <u>in</u> van den Thillart *et al*. 2005, p. 13).

3.7 OUTMIGRATION

Silver American eels leave continental waters in the late summer and fall to undertake an oceanic migration to their Sargasso Sea spawning grounds. The spawning migration occurs in August through October in the northern portions of the range, and from October to December in the mid-Atlantic States, and may continue until March in the southern United States (table 2). In U.S. waters, mature eels may start their outmigration at locations from Maine to the Gulf of Mexico, including much of the Mississippi River basin. During outmigration, American eel move rapidly from freshwater environments to full salinity environments, timing such movements to follow rain events and primarily at night. In the estuary, eels moved at highly variable speeds with a mean rate of about 0.5 body lengths per second, with no preferred water depth (Bradford *et al*. 2009, pp. 287–289, Béguer-Pon *et al*. 2014, p. 1588). Bradford *et al*. (2009, pp. 287–289) noted no preference for tidal cycle, although selective tidal transport of both yellow and silver eels was observed in a nearby estuary with significant tidal forcing (Parker and McCleave 1997, p. 871). Silver eels selectively used nocturnal ebb-tide transport to migrate out of the St. Lawrence estuary (Béguer-Pon *et al*. 2014, p. 1590). European silver eels migrated at night and progressively increased their rate of movement as they moved from the river and through the estuary (Aarestrup *et al*. 2010, pp. 267–268). In the shallow water of the Baltic Sea, silver eels migrated only at night, generally in the upper 0.5 m (1.6 ft), and rested on bottom during daylight in depths of 2 to 36 m (7 to 118 ft) (Westerberg *et al*. 2007, p. 1457). Restocking European eels from outside native Baltic watersheds resulted in silver eels that exhibit the wrong compass orientation in lakes or in the Baltic Sea, such that some silver eels are unable to complete the spawning migration (Wickström 2014, entire), although eels that were translocated within the Baltic Sea retained the proper orientation and migrated normally (Westerberg *et al*. 2014, pp. 152–153).

Little is known about the specific migratory pathways followed by American eels at sea, or about their behavior during migration. Specific routes and swimming dynamics during the

oceanic phase of migration are largely conjectural. Recent tagging studies using satellite tags that pop off after a set period of data collection have demonstrated that European eels retain the negative phototaxis (light avoidance) of yellow eels, exhibiting a diel vertical migration by swimming within 100 m (328 ft) of the surface at night and responding to daylight by descending to 400 m (1300 ft), or in some cases more than 600 m (1970 ft) (Aarestrup *et al.* 2009, p. 1660; Westerberg 2014, p. 91). These telemetry studies also documented that eels rest on the bottom during daylight in shallow portions of the North and Baltic Seas (Westerberg 2014, pp. 86–91). A satellite tag study of American eel conducted in the Gulf of St. Lawrence documented similar diel vertical migrations, although American eels did not dive as deep as European eels and some American eel exhibited reverse diel migration or variable swimming depths (Béguer-Pon *et al.* 2012, p. 6). However, several studies have documented impaired swimming behavior and increased oxygen compensation of dummy-tagged eels in swim-tunnel tests, and concluded that pop-off satellite telemetry tags affected swimming ability and cast some doubt on the reliability of telemetry data collected from migrating eels (Burgerhout *et al.* 2014, p. 633; Methling *et al.* 2011, p. 1). Satellite tagged silver eels that were translocated to the open ocean did not consistently swim at the required speed or orientation needed to reach the Sargasso Sea spawning area (Wysujack *et al.* 2014, p. 156).

American eels travel a much shorter distance to reach the Sargasso Sea than European eels. Actual distances, routes, and depths of migration for adult American eels are unknown but can be estimated assuming a relatively direct migration pathway. Distances traveled by migrating American eels likely vary from under 1,500 km (930 mi) to over 4,500 km (2,800 mi), shorter than the 5,500 km (3,400 mi) or more traveled by European eels. An American eel maturing in the Mississippi River, Louisiana, would travel a distance of over 2,200 km (1,400 mi); from South Carolina, 1,440 km (900 mi); from Chesapeake Bay, Virginia, 1,550 km (960 mi); from Newfoundland, Canada, over 2,800 km (1,740 mi) (McCleave 2001a, p. 805); and from western Lake Ontario, over 4,500 km (2,800 mi).

Energy reserves, particularly stored fat, are required to successfully complete the spawning migration to the Sargasso Sea. Anguilliform swimming is very efficient—four to six times more efficient than other fishes—with greater swimming efficiency correlated with eel size (van den Thillart *et al.* 2009, p. 195). Larger eels also have greater fat stores per body weight, providing them with another migratory advantage. Migrating eels no longer feed, instead relying on energy from stored reserves to complete their migration, as well as to complete gonadal development. A 2009 study of European eel estimated that only 60 g (2 oz) of fat is needed to successfully complete the roughly 5,500 km (3,400 mi) migration from Europe to the Sargasso Sea (van den Thillart *et al.* 2009, pp. 195–196), a remarkably low energy cost. The authors also concluded that because eels consume proteins and fat in the same ratio as present as in their body, tissue depletion during migration does not affect

buoyancy regulation (van den Thillart *et al.* 2009, p. 196), and healthy European eels are able to reach the Sargasso Sea in about 3.5 months with reserves for reproduction.

Gonad development that began in late spring is completed during the marine phase of outmigration. Fecundity varies from about 0.6 million to almost 30 million eggs per female, depending on the size (McCleave 2001a, p. 804). As an example, in the lower Potomac watershed, an average 734 mm (29 in) long female produces 2.7 million eggs, but farther up the watershed, an average female of 870 mm (34 in) produces 5.2 million eggs (Goodwin and Angermeier 2003, p. 533). Size at maturity and fecundity are also linked to growth rate, with more rapidly growing females maturing at smaller size and having greater fecundity for a given size (van den Thillart *et al.* 2005, p. 232; Tremblay 2009, p. 95).

4 HABITAT

American eel are ubiquitous in many habitats, to the extent that they sometimes constitute a large portion of the total fish biomass in many watersheds (Machut *et al.* 2007, p. 1707). American eel habitats include the open ocean, estuaries, large coastal tributaries, rivers, small streams, lakes, and ponds over a range from the east coast of North America, to the northern portion of South America, into the inland areas of the Mississippi River, the Great Lake drainages (primarily Lake Ontario), and north into Canadian tributaries of southern Quebec and the maritime provinces. American eel are sometimes found in landlocked lakes, particularly in the northeastern United States (Facey and Van den Avyle 1987, p. 16). American eel are thought to occupy the broadest array of habitats of any fish in the world (Helfman *et al.* 1987, p. 42).

American eel use a variety of marine and freshwater habitats at different life stages. Eel larvae rely upon ocean currents to return to continental waters, while silver eels use riverine, estuarine and marine habitats during their migrations to the Sargasso Sea. In fresh water, preferred habitat is found in lakes and rivers to depths of at least 10 m (33 ft). In marine habitats, the continental phase includes predominantly shallow, protected waters in estuaries and near-shore habitats. Growing eels are primarily benthic, using substrate (rock, sand, mud), large wood and submerged vegetation for protection and cover, particularly in daylight. Freshwater overwintering habitat is not well documented, but yellow eels have been observed to overwinter in mud bottoms in both fresh water and estuary habitats.

4.1 REPRODUCTIVE AND LARVAL HABITAT

Water temperature and salinity are possibly the most important habitat characteristics that determine spawning locations and larval habitat of American eel. As described in section 3.2, American eel spawn in warmer, higher salinity, waters south of thermal fronts that they encounter in the Sargasso Sea to the south of the Sub-Tropical Convergence Zone (Kleckner *et al.* 1983, p. 289; Kleckner and McCleave 1988, pp. 647–648; Tesch and Wegner 1990 p. 845, Munk *et al.* 2010, p. 3595). The northern limit of spawning in the Sargasso Sea is thought to occur in areas where the water temperatures are characterized by 18 to 19°C (64 to 66°F) isotherms at depths between 200 and 300 m (660 to 980 ft) (Kleckner and McCleave 1988, p. 662–663). The salinity of these Sargasso Sea spawning areas tend to be greater than 36.6 ppt (Kleckner and McCleave 1988, p. 662–663). Water depths are typically thousands of meters.

4.2 YELLOW EEL HABITAT

Consistent with the definition of catadromy, most juvenile American eel are found in freshwater habitats. However, American eel catadromy is now viewed as facultative since juvenile eels are not restricted to fresh water, but also use marine and estuarine habitats

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(Tsukamoto *et al.* 2002, p. 1992; Jessop *et al.* 2002, pp. 226–228; Lecomte-Finiger 2003, p. 265; McCleave and Edeline 2009, p. 69). In fact, Cairns *et al.* (2009, p. 2109) suggest that the use of freshwater habitats by anguillid eels is a paradox since growth rates are higher in saltwater habitats. Suitable juvenile American eel rearing habitats are found in: (1) lakes and streams, (2) brackish water estuary habitats, and (3) full-salinity near-shore habitats (Morrison *et al.* 2003, pp. 90–92; Lamson *et al.* 2006, p. 1567; Cairns *et al.* 2009, pp. 2106–2109). Based on strontium:calcium concentration ratios in otoliths, Jessop *et al.* (2008, p. 205) determined that 12 to 25 percent of yellow eels entered fresh water after an initial growth period in saltwater, and up to 77 percent of yellow eels left fresh water in favor of saltwater habitats. However, the authors found that these interhabitat migrations typically occur only once, and they are more common among juvenile eels in close proximity to saltwater—that is, exclusive fresh water residence increases with distance of upstream movement. McCleave and Edeline (2009, pp. 102–103) documented similar patterns among European yellow eels—variable habitat use histories among eels captured in estuaries and coastal habitats, and near exclusive freshwater habitat use among eels captured in fresh water.

4.2.1   ESTUARY AND MARINE HABITATS

Yellow eels use estuaries and adjacent near-shore marine habitats (Helfman *et al.* 1984, p. 135; Jessop *et al.* 2002, pp. 84, 228; Morrison *et al.* 2003, pp. 93–95, 97; Knights *et al.* 2006, pp. 12–13). An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage tributaries. Yellow eels in freshwater habitats may use estuaries for periods of time to optimize growth since inshore coastal and estuarine productivity is greater than that of rivers and lakes (Knights *et al.* 2006, p. 25). With regard to full salinity marine habitats, juvenile American eels can use high salinity habitats but may prefer brackish waters—Geer (2003, p. 101) documented that 89 percent of Chesapeake Bay juvenile eels were caught in less than 12 ppt salinity, and Dutil *et al.* (1988, p. 488) found that telemetered yellow eels selected salinities of less than 12 ppt in estuaries despite the availability of adjacent waters with up to 24 ppt salinity. Jessop *et al.* (2008, p. 205) report that 12 to 25 percent of American eel recruit to fresh water as juveniles, rather than elvers.

Estuarine habitat includes a mix of males and females. Because eels grow faster in estuarine waters than fresh water, the average age of a female within estuarine waters preparing to spawn is much younger (approximately 9 years of age) than females leaving lake habitats (e.g., 24 years of age in Lake Ontario). As stated above, variation in maturation age benefits the population by allowing different individuals of a given year class to reproduce over a period of many years, which increases the chances of encountering environmental conditions favorable to spawning success and offspring survival. Jessop *et al.* (2002, p. 228) provides an interesting perspective on the relative production of silver

eels by comparing elvers that spend 1 to 4 years in the estuary versus elvers that entered the river shortly after continental arrival. The authors suggested that the relative production of silver eels was 380 times higher for juvenile eels that spent 1 or more years in estuaries than in fresh water, due to better growth rate in the estuary and possibly lower mortality. Helfman *et al*. (1984, p. 135) noted that estuarine habitat provided more favorable annual growing conditions—maximum size was greater in fresh water, but lengths at a given age were greater in estuaries. Morrison *et al*. (2003, pp. 94–95) found that annual growth rates were approximately twofold higher in brackish water when compared to annual growth rates in fresh water. The theory is that eels that grow faster emigrate earlier. Facultative catadromy is common among all of the anguillid eels. However, American eel more than double their growth rate in brackish water, whereas *Anguilla anguilla, A. japonica* and *A. australis* have only a 13 percent mean growth rate increase in saltwater (Cairns *et al*. 2009, p. 2103).

4.2.2   FRESHWATER HABITAT

Yellow eels are highly adaptive ecologically and will use many types of lotic (moving water) and lentic (still water) freshwater habitats (McCleave 2001a, p. 800). Yellow eels are found in higher density below barriers such as small dams, than above them and grow at a faster rate when they reach upstream habitats (Machut *et al*. 2007, p. 1707; Bowser *et al*. 2013, p. 11). They are primarily benthic and use a variety of substrates including rock, sand, mud, large wood, and submerged vegetation for protection and cover, particularly in daylight. They are habitat generalists with little consistent preference for habitat type, cover, or substrate (Wiley *et al*. 2004, p. 520). In Maryland, Wiley *et al*. (2004, p. 520) observed a weak relationship between eel density and diversity of water depths/velocities. The authors also found that smaller eels were associated with faster currents while larger eels were associated with slow, deep habitats (Meffe and Sheldon 1988, <u>in</u> Wiley *et al*. 2004, p. 520). In New York, Machut *et al*. (2007, p. 1707) found smaller eels associated with cobble and gravel, and larger eels associated with larger cobbles, boulders, and sand. Lloyst (2012, <u>in</u> Pratt *et al*. 2014, p. 7) found larger eels within larger substrates such as boulders and argued that, although yellow eels may be habitat generalists, they have size-specific substrate preferences—this idea is supported by the fact that the yellow eels establish a home range (Dutil *et al*. 1988, p. 488; Oliveira and McCleave 2000, p. 150). Yellow eels can also be found in soft sediments where they burrow in the sediments, or shelter within aquatic macrophytes to avoid predators (Tomie *et al*. 2013, p. 287).

Since yellow eels inhabit both lotic and lentic waters, they can tolerate a wide range of velocity and depth conditions. Solomon and Beach (2004, pp. 15, 17) describe burst speeds of 8 cm (3.2 in) European elvers as 0.5 m/s (1.6 ft/s) and burst speed of eels in the 400 to 600 mm (16 to 24 in) length range as about 1.3 m/s (4.3 ft/s). Thus, eels have the capability to move upstream through fast moving stream reaches. Most studies have found water

velocity to be of little or no predictive value for eel occurrence, though size-specific habitat preferences were noted with larger eels preferring slow, deep habitats and smaller eels preferring faster currents in one study (Meffe and Sheldon 1988, in Wiley et al. 2004, p. 520), and the presence of a variety of velocity-depth habitats were found to be important for modeling eel presence in Maryland rivers (Wiley et al. 2004, p. 520). Upstream movement may also be impeded or obstructed by high velocity currents, though flow velocities that restrict movement are poorly understood. During upstream migration, movement tends to occur during periods of low water velocity, typically midsummer.

American eels are tolerant of a wide range of water temperatures. For example, Geer (2003, pp. 109–111) captured eels in Chesapeake Bay at temperatures ranging from 3 to 31°C (37 to 88°F), with the highest proportion of eel catch from 26 to 28 °C (79 to 82 °F). In laboratory settings, Barila and Stauffer (1980 in Geer 2003, p. 109) identified a preferred temperature of 16.7°C (62°F), similar to the 17 to 20°C (63 to 68°F) preference range found by Haro (1991, p. 171). Tzeng et al. (1998, p. 111) found the maximum growth of American eel at 28 to 29°C (82 to 84°F). In the European eel, Nyman (1972, in Pratt et al. 2014, p. 7) documented an optimal summer feeding temperature range of 13 to 17°C (55 to 63°F), with higher temperatures leading to aggressive behavior, and Sadler (1979, in Pratt et al. 2014, p. 7) documented an optimal temperature range of 22 to 23°C (72 to 73°F) in the lab—both of these ranges are similar to the American eel. In winter, some American eels take refuge in soft substrates and enter torpor in cooler water temperatures. For example, Walsh et al. (1983, p. 532) held yellow eels at 5°C (41°F) for over five weeks, and found that at temperatures less than 8°C (46°F) they stopped feeding and remained inactive for months.

Suitable freshwater habitat for yellow eels may be limited by low dissolved oxygen levels. In North Carolina, yellow eels were nearly always caught in waters with dissolved oxygen levels above 4 parts per million (ppm) (Rulifson et al. 2004, in Pratt et al. 2014, p. 8). Less than 2 percent (122 of 7182) of the eels captured in Chesapeake Bay by Geer (2003, p. 111) were at sites with dissolved oxygen levels less than 4 ppm.

American eels are opportunistic benthic feeders that forage primarily at night and consume mostly macroinvertebrates (figure 8). Food type varies with body size—eels less than 400 mm (16 in) long consume a wide variety of aquatic insects and large eels ingest more crayfish and fish (Stacey 2013, in Pratt et al. 2014, p. 8).
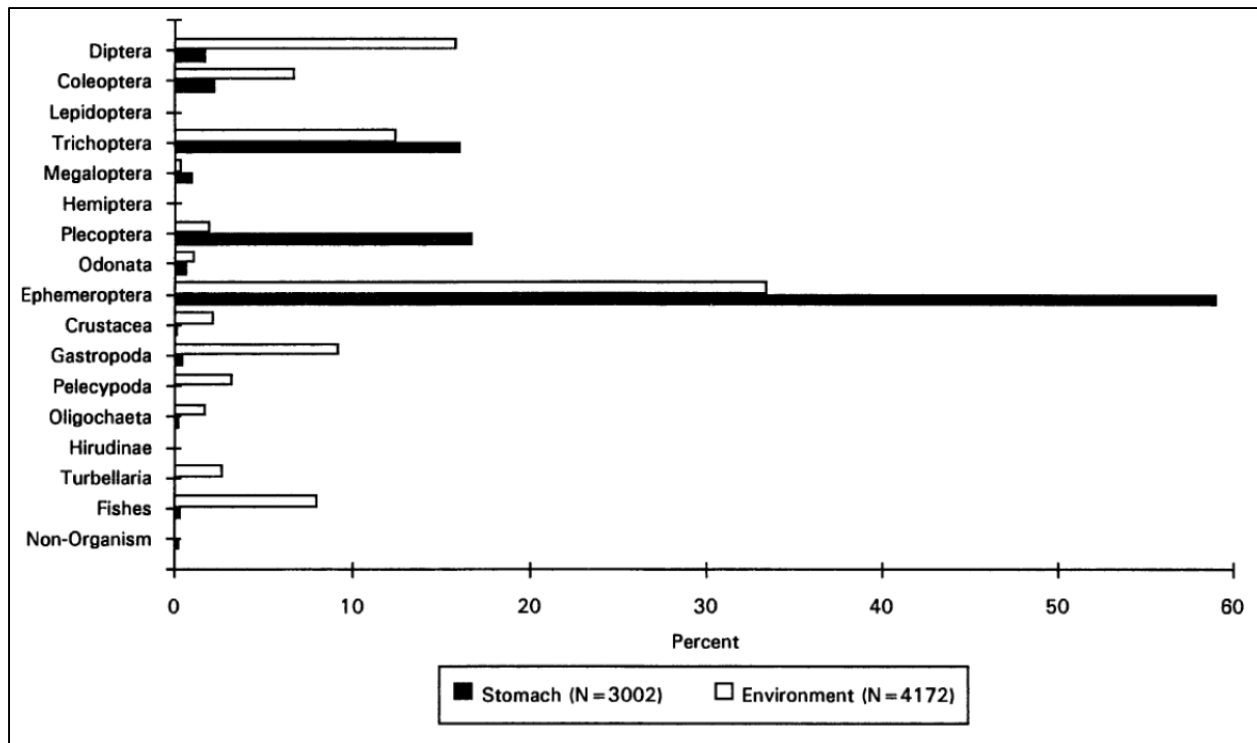
FIGURE 8—Relative abundance (percent) of items observed in samples from the prey base found in the upper Delaware River and American eel stomachs during May to August 1986 (from, Denoncourt and Stauffer 1993, p. 306).

4.3   DENSITY DEPENDENCE IN REARING HABITATS

Density dependent competition may act upon young eels at the time of river entry, when large numbers of elvers arrive from marine waters, or when the biomass of growing yellow eels has exceeded the carrying capacity of a particular habitat, forcing yellow eels to disperse into less crowded areas (Feunteun *et al*. 2003, pp. 201–204; Ibbotson *et al*. 2002, p. 1703). As young eels begin to grow, density dependent competition prompts eels to disperse into less crowded areas (Feunteun *et al*. 2003, pp. 201–204) and growing eels, particularly females, disperse to upstream habitats over time (Ibbotson *et al*. 2002, pp. 1703–1704). Aggressive interactions at high density inhibit feeding and growth, but stimulate dispersive swimming activity in smaller eels (Knights 1987 *in* Knights *et al*. 2006, p. 10), the latter likely as a defense against predation. As the size differences among juvenile eels increase, cannibalism can be a source of mortality (Knights 1987 in Knights *et al*. 2006, p. 10). Density dependent dispersion ensures wider distributions, further minimizing intra-specific competition. Benefits of density dependent dispersion include selection of optimal habitat productivity and temperature, lower predation risks, rapid colonization or re-colonization of habitats, and avoidance of inter-specific competition. Farther upstream, eel density declines, larger individuals are more common, females predominate, eels are more sedentary, and they occupy specific territories (Feunteun *et al*. 2003, p. 201).

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Within watersheds, eel density decreases further inland and females are more common (see section 3.5). Eel density decreases with distance from the coast, likely as a result of density dependent dispersion (Smogor *et al*. 1995, p. 799; Knights 2001 <u>in</u> Knights *et al*. 2006, p. 8). As eel density decreases, the female proportion increases—assuming that the abundance of females limits population growth, then shifting sex ratios toward females at low abundance is a compensatory mechanism during times of low eel abundance (Knights *et al*. 2006, pp. 11–13). Furthermore, although mean watershed densities decrease by an order of magnitude with distance inland from the coast, mean biomass declines by only about 50 percent because of the larger size and relative fecundity of female eels (Knights *et al*. 2006, p. 10).

4.4 SUMMARY

Spawning American eel, and early larval stages, require specific seasonal habitats that occur only in certain locations in the Sargasso Sea. The location of these habitats varies from year to year within the southwest Sargasso Sea. Spawning is associated with warm sub-tropical, high salinity, waters that produce thermal fronts with regions of specific thermal gradient. These sub-tropical waters have low primary productivity, and contain few predators that might consume larvae, but produce enough organic detritus (i.e., marine snow) to sustain larvae. Equally important, the dominant ocean currents in this region passively carry larvae towards continental waters that support juvenile growth.

Many types of habitats found in continental waters will support yellow eel growth. Suitable habitats include estuaries with wide ranges of salinity and nearly any accessible freshwater habitat. In fresh waters, juvenile eels are found in a diversity of lentic habitats from large main-stem rivers to headwater streams, and lotic habitats of various trophic states and types. Juvenile eels may move among these habitats at any time. Habitat characteristics and juvenile eel life history are intrinsically linked. That is, sexual determination, growth rate, and age/size at maturation are all linked to the productivity of a habitat, the density of juvenile eels within that habitat, and the stimuli that result in migration to a different habitat type. Whether habitat determines life history, or yellow eels select habitats appropriate to their life history, is one of the mysteries of this fascinating species.

5 STATUS

American eel are found in much of the Mississippi River watershed and all of the states eastward. Figure 9 shows the distribution of American eel in the United States based upon current fish survey data (e.g., electrofishing, trapping, and netting) provided by state regional fish biologists, recent eel fishway construction, NatureServe (2013) data, current records of eel stocking, and published distribution records. As described in the 2007 Finding (72 FR 4267), no rangewide estimate of American eel abundance exists. Information on demographic structure is lacking and difficult to determine because the American eel is a single panmictic population with individuals randomly spread over an extremely large and diverse geographic range, with growth rates and sex ratios environmentally dependent. Because of this unique life history, site-specific information on eels must be evaluated in context with its significance to the entire population. Determining population trends is challenging because the relevant available data are limited to a few locations that may or may not be representative of the species' range and little information exists about key factors such as mortality and recruitment that could be used to develop an assessment model. Furthermore, the ability to make inferences about species' viability based on available trend information is hampered without an overall estimate of eel abundance. Despite these challenges, the following sections describe our understanding of the status of the species based on the best available data.
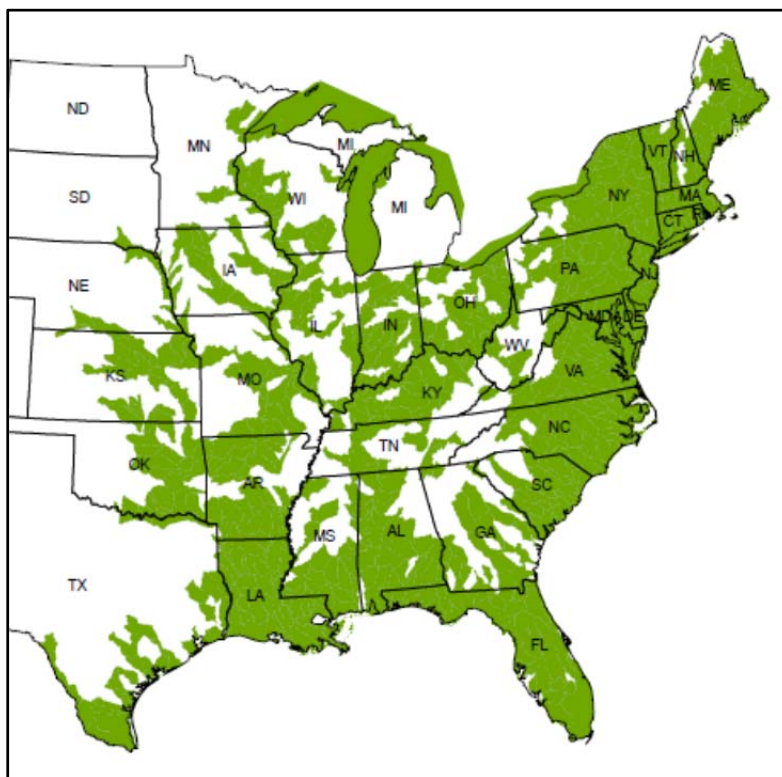
FIGURE 9—Current American eel distribution in the continental
United States based on presence or absence in HUC 8 watersheds.

Commercial harvests are depicted in figure 10. Commercial eel landings are primarily yellow eels, but also include silver and glass eels caught in both fresh water and marine fisheries. Even in states with mandatory reporting, the reporting requirements may only include the marine district, resulting in a potential underestimate of total landings. In addition, market conditions and economic opportunities for commercial fishers have significant effects on eel landings that are independent of eel population abundance. As a result, eel landings are not expected to be reflective of eel abundance.
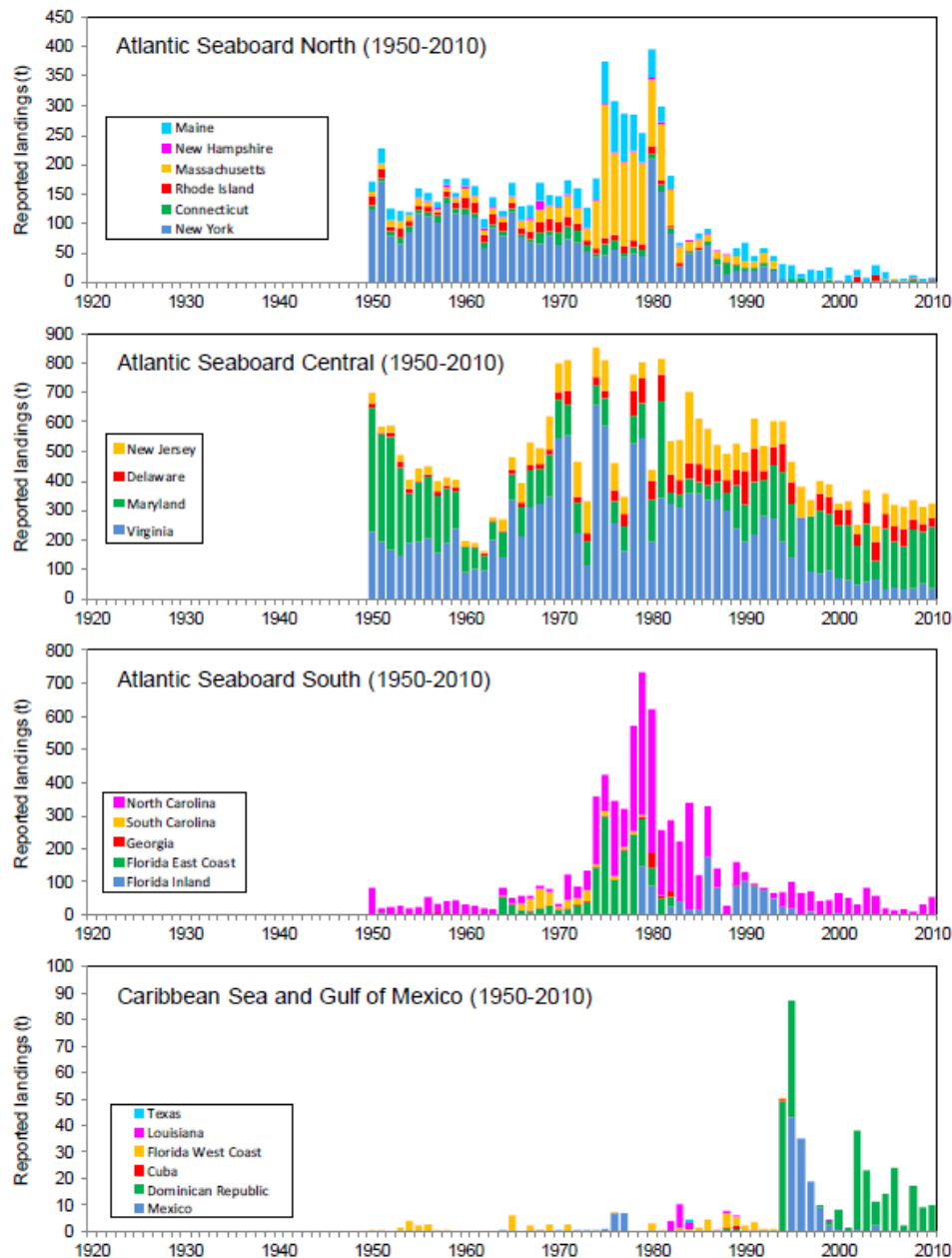
FIGURE 10—Commercial landings of American eel in the U.S. Atlantic Seaboard, the Caribbean Sea, and the Gulf of Mexico, 1950 to 2010 (from Cairns *et al*. 2014, p. 108). Vertical axes show tons of eels landed with different scales.

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5.1 ASMFC STOCK ASSESSMENT

The Atlantic States Marine Fisheries Commission (ASMFC) is a commission of U.S. Atlantic coast states that was formed to coordinate and manage fishery resources, including marine fish, shellfish, and diadromous fish such as the American eel. The ASMFC Benchmark Stock Assessment (SA) for American eel was completed and accepted for management use in 2012. The SA is based on glass, elver, and yellow eel abundance data through 2010. The SA indicated that the American eel stock has declined in recent decades and the prevalence of significant downward trends in multiple surveys across the Atlantic coast caused the ASMFC to declare the stock to be depleted (ASMFC 2012, entire). The ASMFC American Eel Technical Committee (TC) and Stock Assessment Subcommittee (SAS) caution that although commercial fishery landings and effort have declined from high levels in the 1970s and 1980s (with the recent exception of the glass eel fishery), current levels of fishing effort may still be too high given the additional stressors such as habitat loss, passage mortality, and disease as well as potentially shifting oceanographic conditions affecting the stock. Fishing on all life stages of eels, particularly active fisheries for glass and silver eels, could be particularly detrimental to the stock, especially if other sources of mortality (e.g., turbine mortality, and changing oceanographic conditions, see sections 6.4 and 6.1, respectively) cannot be readily controlled.

In 2014, the TC and SAS completed an update of the YOY indices included in the SA (table 3). The Fisheries Management Plan (FMP) requires most states and jurisdictions with a declared interest in the species to conduct an annual YOY survey for the purpose of monitoring annual recruitment of each year's cohort. The SA included data only through 2010. Since that time, some states have heard anecdotal information about increased recruitment as well as recorded evidence of increased recruitment in their fisheries independent YOY surveys, as described in the following sections.

Based on the update of the YOY indices, the TC found no change in the YOY status from the SA with the exception of one survey in Goose Creek, South Carolina, which possibly represents the closest YOY monitoring site to the spawning grounds. The YOY trends are influenced by many local environmental factors, such as rainfall and spring temperatures. While some regions along the Atlantic coast have experienced high catches in 2011, 2012, and/or 2013, other regions have experienced average or lower catches. For example in 2012, Rhode Island and Florida had below average counts, with Florida having its lowest catch of their time series; New Hampshire, New York, Virginia, and Georgia had average counts; and Maine, Connecticut, New Jersey, Delaware, and Maryland had their highest YOY catches on record. The TC has emphasized that high YOY catches in a few consecutive years do not necessarily correspond to an increasing trend since the YOY surveys typically have high variability (figure 11). Due to the limited extent of sampling, trends at the state level may not be reflective of what is actually occurring statewide, or even in watersheds adjacent to sample sites, nor reflective of what may be occurring

TABLE 3—ASMFC (2014a) update of the YOY trend analyses. Mann-Kendall trend analysis tests are applied to the 2012 Benchmark Stock Assessment and updated YOY indices. Trend indicates the direction of the trend if a statistically significant temporal trend was detected (P-value < α; α = 0.05). NS = not significant.

| Region	State	Site	SA Result	Update
Gulf of Maine	ME	West Harbor Pond	NS	NS
	NH	Lamprey River	NS	NS
	MA	Jones River	NS	NS
	MA	Parker River	NS	NS
Southern New England	RI	Gilbert Stuart Dam	NS	NS
	RI	Hamilton Fish Ladder	NS	NS
	NY	Carmans River	NS	NS
Delaware Bay/ Mid-Atlantic Coastal Bays	NJ	Patcong Creek	NS	NS
	DE	Millsboro Dam	NS	NS
	MD	Turville Creek	NS	NS
Chesapeake Bay	PRFC	Clarks Millpond	NS	NS
	PRFC	Gardys Millpond	NS	NS
	VA	Brackens Pond	NS	NS
	VA	Kamps Millpond	NS	NS
	VA	Warehams Pond	NS	NS
	VA	Wormley Creek	NS	NS
South Atlantic	SC	Goose Creek	NS	↓
	GA	Altamaha Canal	NS	NS
	GA	Hudson Creek	NS	NS
	FL	Guana River Dam	NS	NS
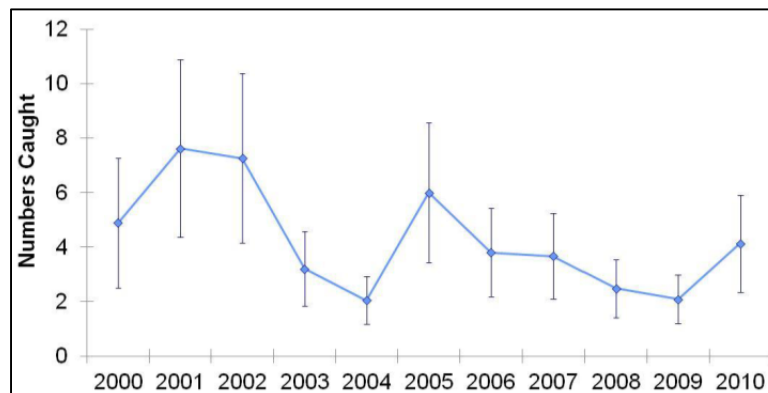
FIGURE 11— The coast-wide short-term YOY index (2000 to 2010) used in the ASMFC benchmark stock assessment. The index combines the YOY standardized indices derived from the ASMFC-mandated annual recruitment surveys. From ASMFC 2014a, p. 8.

coastwide. The YOY indices were only one factor in the determination of the depleted stock status for American eel; therefore the TC did not recommend a change in the conclusions of the SA and the eel stock is still considered to be depleted.

State reported landings of yellow/silver eels in 2013 totaled 416,150 kilogram (kg) (917,454 pounds (lbs)) which represents a 17 percent decrease from 2012 landings. Since 2000, yellow eel landings have increased in the mid-Atlantic region (NY, NJ, and MD) with the exception of Delaware and the Potomac River. Additionally, yellow eel landings have declined in the New England region (ME, NH, MA, CT) with the exception of Rhode Island. Within the Southern region, since 2000, landings have declined in North Carolina but increased in Florida. In 2013, State reported landings from New Jersey, Delaware, Maryland, and Virginia each totaled over 36,000 kg (80,000 lbs) of yellow eel, and together accounted for 86 percent of the coastwide commercial total landings. Addendum IV of the ASMFC management plan limits yellow eel fisheries to a 2015 quota of 907,671 lbs, with a 2015 quota of 9,688 pounds for the Maine glass eel fishery. Glass eels are exported to Asia to serve as seed stock for aquaculture facilities and glass eel fisheries are only permitted in Maine and South Carolina. Maine is the only State reporting significant harvest and the 2015 fishery is contingent on a requirement to implement a fishery-independent study of the eel life cycle. In addition to these United States fisheries, glass eels are harvested in the Dominican Republic, Haiti (Benchetrit and McCleave 2015, p. 9), and the Canadian provinces of Nova Scotia and New Brunswick.

5.2 ATLANTIC SEABOARD NORTH

Maine: American eel are found throughout Maine, with the exception of the Upper St. John River. Our knowledge of current distribution of American eel for the Androscoggin and Kennebec watersheds of Maine and New Hampshire is based on a systematic survey in 2002 and 2003, and supplemental electrofishing survey data (Yoder *et al.* 2006, pp. 35–94). Presence of eel fishways on dams has increased eel abundance in these watersheds in the last decade. Maine in one of two states that has a glass eel fishery on the U.S. East Coast and, since 1998, more than 90% of the total glass eel harvest has come from the state (South Carolina has a very small glass eel fishery, see Section 6.5.1 for descriptions and analyses of glass eel fisheries). According to the Maine Department of Marine Resources (www.maine.gov/dmr), the harvest increased in 2011 to 2014 in response to market prices that rose to peak prices of more than $2,000 per lb paid to the glass eel fishers. However, 2014 prices were reportedly down to between $400 and $650 per lb (Bangor Daily News 2014, p. 2). Landings of glass eels reported from Maine were 9,414 kg (20,753 lbs) in 2012 and 8,280 kg (18, 253 lbs) in 2013—early harvest estimates indicate that the lower price paid in 2014 reduced the Maine harvest to 4,475 kg (9,866 lbs), well below the 11,749 lb quota set by the ASMFC. High prices for glass eels have created poaching concerns in states that do not have legal glass eel fisheries (Bangor Daily News 2014, p. 2).

New Hampshire: In 2001, the State of New Hampshire Department of Fish and Game (NHDFG) established an annual survey of YOY eels migrating up the Lamprey River in Newmarket, NH as part of the ASMFC American Eel Technical Committee standard sampling protocol for YOY abundance estimates and trends (NHDFG 2013). Glass eels at this site are generally 45–70 mm (1.8–2.8 in) and elvers are 65–100 mm (2.6–3.9 in). Abundance at this index site has been extremely variable with the largest catch in 2013 (figure 12). In 2013, another YOY survey site was added in NH on the Oyster River in Durham.
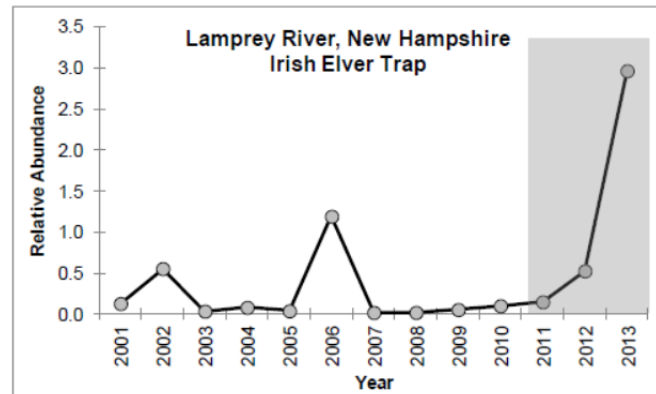
FIGURE 12—Relative abundance of elvers captured at the New Hampshire YOY index site (ASMFC 2014a, p. 1).

Massachusetts: A yellow eel fishery in Massachusetts targets eels for food and bait (ASMFC 2014, unpublished data). From 1950 through the early 1990s, the annual reported landings averaged about 30,000 pounds with the exception of a nine year period (1974-1982) when landings averaged 280,000 pounds due to an increase in demand from the export market. Since 2009, the eel fishery has declined to historical lows, with landings under 2,500 pounds. YOY surveys were conducted in the Jones River since 2001 and the Parker River since 2004. The Jones River YOY catch has shown a fairly flat trend that may be declining slightly, while the Parker River YOY catch has shown an increasing trend.

Rhode Island: According to the ASMFC (2014, unpublished data), there are very few directed commercial fisheries for yellow eel in Rhode Island and landings have been under 5,000 pounds since 2009. YOY surveys have been conducted at the Gilbert Stuart dam in the Pettaquamscutt River since 2000 and at Hamilton Fish Ladder on the Annaquatucket River since 2004. Catches have been higher at the Gilbert Stuart site where they peaked in 2011. YOY catches were also high in 2013.

Connecticut: According to the ASMFC (2014, unpublished data), most waters in the state of Connecticut historically supported American eel and there have been yellow eel pot fisheries in Connecticut since colonial times. Currently, that fishery is only permitted in

tidewater areas and in the Connecticut River between Hartford and Long Island Sound. Landings have been less than 5,000 pounds since 2009, with anecdotal information from eel potters that the majority of harvest is used for bait. YOY monitoring occurs at 12 eel passage facilities in the state including the index site at Ingham Hill Dam in Old Saybrook.

New York: According to the ASMFC (2014, unpublished data), yellow eel landings have increased from a low of 3,881 pounds in 2003 to 32,573 pounds in 2013. However, landings data are believed to be underestimated. The state's YOY survey has been conducted since 2000 at Carman's River, located on the south shore of Long Island. Total catch of glass eels has varied over time with the highest catch (13,491) occurring during 2002. A citizen's science monitoring project is also conducted along several tributaries of the Hudson River.

New Jersey: American eel are ubiquitous in New Jersey waters (N.J. Division of Fish and Wildlife, unpublished data). According to the ASMFC (2014, unpublished data), yellow eel landings have decreased from a high of 164,331 pounds in 2007 to a low of 89,300 pounds in 2013. The majority of landings (81%) are going to the food market. Since 2000, YOY sampling has occurred at Patcong Creek in Linwood, NJ which flows into the Great Egg Harbor, Great Egg Inlet and finally to the Atlantic Ocean. YOY catches have been low but stable since 2000, with high catches in 2002, 2006, and 2012.

5.3 ATLANTIC SEABOARD CENTRAL

Eels are distributed throughout tidal and freshwater habitats of the Chesapeake Bay and tributaries and Atlantic coast. Commercial pot fisheries in Maryland, Delaware, and Virginia account for a large portion of the coastwide commercial yellow eel harvest. Harvest is limited to tidal waters. A large natural barrier (Great Falls) limits the distribution of eels to the headwaters of the Potomac River. On the lower mainstem of the Susquehanna River, the Conowingo Dam at river km 10 (river mi 6) blocks eel migration into most of the watershed of the largest tributary of the Chesapeake. Large water supply dams block eel migrations in several tributaries to the Bay.

Virginia: American eels are widely distributed in Chesapeake Bay and Virginia tributaries. Removal of Embry Dam in 2004 on the Rappahannock River showed that eel abundance increased in the headwater tributaries following dam removal (Hitt *et al*. 2012, entire) and other dam removals, such as Harvell Dam on the Appamattox River in 2014 will also likely benefit eel populations within the State. There is an active commercial fishery in the Chesapeake Bay and lower tributaries in Virginia, with annual landings between 60,000 and 120,000 lbs in the last decade (figure 13). Two YOY surveys are conducted annually in the York (Brackens Pond) and Rappahannock (Kamps Millpond) rivers. Collections have been variable and no trend in recruitment is evident between 2000 and 2013 (ASMFC unpublished data).
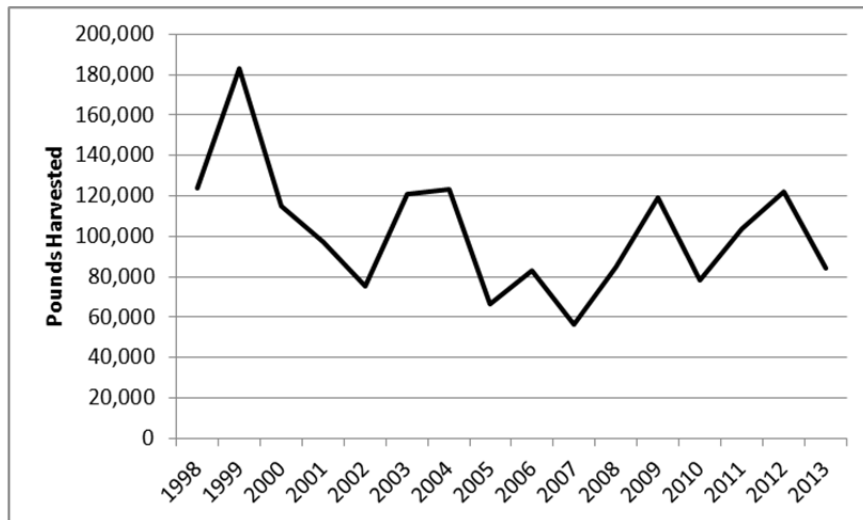
FIGURE 13—Virginia commercial eel landings data (1998 to 2013) (data from ASMFC 2014b, p. 10).

Potomac River: American eel are distributed throughout the Potomac River Basin in West Virginia, Virginia, Maryland and Pennsylvania. Eel abundance is high in the lower section of the river and lower in locations above a waterfall known as Great Falls (Goodwin and Angermeier 2003, pp. 525, 532). There is an active yellow eel fishery in the lower Potomac River (ASMFC 2014b, p. 10; Fenske *et al*. 2011, p. 1035), and harvests have declined in recent years, with landings less than 100,000 lbs annually since 2005 (figure 14) (ASMFC
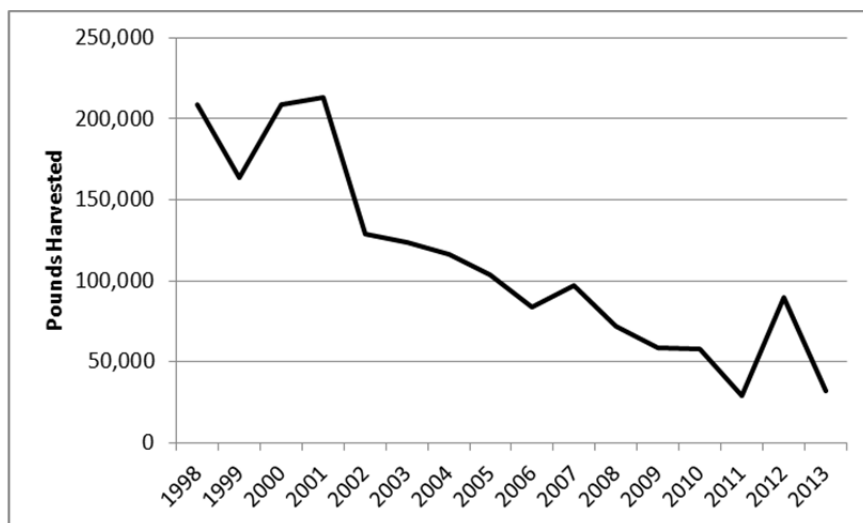
FIGURE 14—Potomac River commercial eel landings data (1999 to 2013) (data from ASMFC 2014b, p. 10).

2014b, p. 10). American eel YOY surveys for the lower Potomac River have been conducted at two locations since 2000. Catch rates are variable in the surveys and there has been no trend in recruitment to the Potomac River over the time series.

Maryland: American eels are abundant in the Chesapeake Bay and tributaries as well as in the Atlantic Coastal Bays in the state of Maryland. There is a substantial commercial fishery in the Maryland portion of the Chesapeake Bay that targets the yellow phase of American eels (Weeder and Uphoff 2009, entire). Commercial landings in Maryland are the largest in the U.S. and have exceeded 227,000 kg (500,000 lbs) annually since 2010 (ASMFC 2014b, p. 10) (figure 15). A YOY survey has been conducted annually in Turville Creek in the Coastal Bays of Maryland and catches have been variable from 2000 through 2013, with no discernable trend in recruitment (ASMFC 2014b, p. 8).
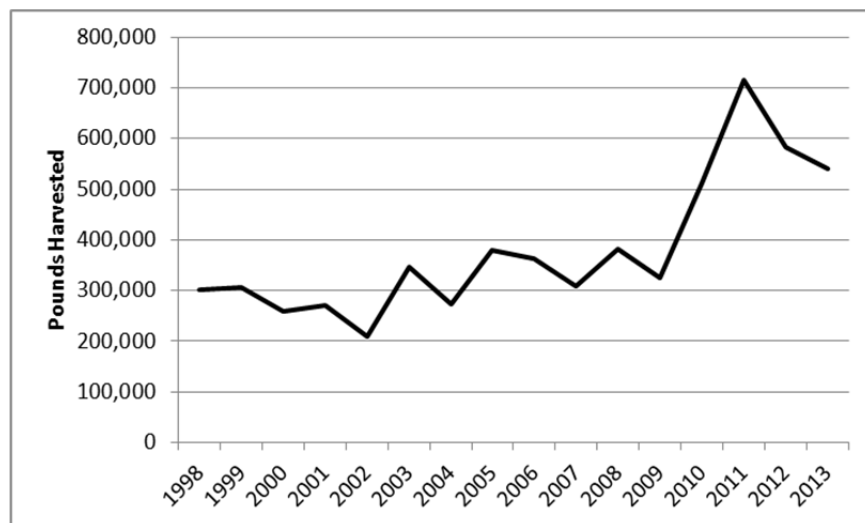
FIGURE 15—Maryland commercial eel landings data (1999 to 2013) (data from ASMFC 2014b, p. 10)

West Virginia: West Virginia is comprised of three major river basins. On the west slope of the Appalachian Mountains, eels have been collected in the Ohio River basin from the Kanawha, New, and Greenbrier rivers, although there are no records since 1995 (West Virginia Division of Natural Resources (WVDNR) 2011, entire). East of the Appalachian divide, the James and Potomac Rivers flow from West Virginia to Chesapeake Bay. American eels occur throughout the Potomac River watershed (Stauffer *et al*. 1995, p. 44). There are no recent records of American eel in the West Virginia portion of the upper James watershed (WVDNR 2011, entire). No commercial fishery for American eel exists in West Virginia and various fishery surveys provide limited eel abundance information.

Pennsylvania: There is no active commercial eel fishery in Pennsylvania. Eel are found in the Potomac, Susquehanna and Delaware River drainages of the Atlantic Coast and the Ohio River Drainage of the Mississippi River. No abundance estimates are available for American eels in these river systems and eels are not targeted in any surveys at this time.

Susquehanna River: American eels have been precluded from the Susquehanna River since the construction of the lower mainstem dams in the early 1900's (Susquehanna River Anadromous Fish Restoration Cooperative (SRAFRC) 2013, p. 3). Stocking efforts by the State of Pennsylvania from 1936 through 1980 resulted in some eels being present within the basin (SRAFRC 2013 p. 13). No stocking was conducted between 1980 and 2008, and eel passage at the fish lifts was very low (less than 15 annually, SRAFRC 2013 p. 14) such that eels were essentially extirpated from the system for over 20 years. Efforts to develop upstream passage were initiated by the Service in 2005 and in 2008, when the Service began a trap and transport program at Conowingo Dam. Nearly 750,000 American eel elvers were collected and stocked in upstream locations between 2008 and 2014 (SRAFRC 2013, p. 14). Most of the eels were captured during June, July and August and were between 80 and 150 mm (3.1 to 5.9 in). The FERC relicensing at Conowingo Dam may provide eel passage facilities to support long-term restoration of eels into the Susquehanna River watershed.

Delaware: American eels are abundant in the Delaware Bay and in the Delaware Coastal Bays. There is an active fishery for yellow eels in the Bay and tributaries. Commercial landings have ranged from roughly 27,000 to 41,000 kg (60,000 to 90,000 lbs) annually since 2008 (figure 16) (ASMFC 2014a, p. 10). The annual YOY is conducted on Millsboro Pond Dam, located on a tributary to the coastal Indian River Bay. Recruitment from the
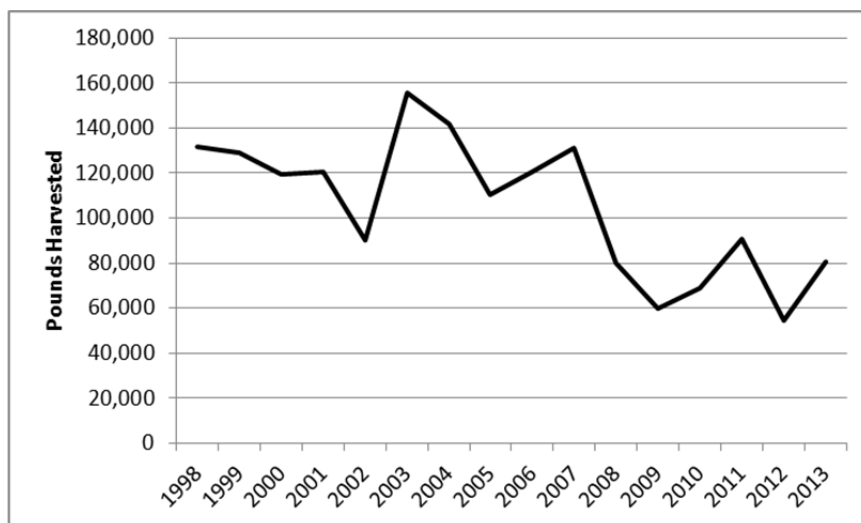
FIGURE 16—Delaware commercial eel landings data (1999 to 2013) (ASMFC 2014a, p. 10).

YOY survey since 2000 shows relatively stable recruitment for the first 12 years of the survey and the 2013 catches were abnormally high. However, there are no trends in recruitment at this location for the duration of the survey.

5.4   ATLANTIC SEABOARD SOUTH

South of the Chesapeake Bay, American eel are widely distributed in coastal and inland waters up to the first impassable barrier (typically a hydroelectric dam). Commercial fisheries in the States of North Carolina, South Carolina, Georgia, and Florida harvested in excess of 200 tons of American eel annually from the late 1970s through early 1980s (figure 10). Only North Carolina continues a small commercial eel harvest.

North Carolina: At Roanoke River in North Carolina, upstream migration patterns are emerging from annual passage counts at the first dam, and American eels are abundant with 1.9 million eels passed between 2010 and 2013 (Dominion Electric Environmental Services 2014, p.3). Catch rates were highest when tailwater temperatures were 17 to 25°C (63 to 77°F). Most of these eels captured were between 180 to 229 mm (7 to 9 in) at this site located 220 km (137 mi) inland.

South Carolina: Within South Carolina, eels occur from estuaries to the headwaters of coastal streams and far inland above the fall line in some of the larger river basins, including the Savannah and Pee Dee Rivers (figure 17). Although the American eel is capable of traversing obstacles that may completely restrict dispersal of other fishes, both eel distribution and population size may be limited by dams and other impediments to migration. Historical records show that American eels occurred in the Santee basin well inland of the fall line and into North Carolina. Similar historical distributions occurred for the Waccamaw-Pee Dee River

FIGURE 17—American eel density in South Carolina watersheds (from S. Carolina Dept. Natural Resources).

basin and eels were likely to be present in the Savannah River basin. Fishway counts in the Santee River basin upstream of the first dam revealed patterns in passage by juvenile eels, with most fish delayed at the first dam (Bulak and Bettinger 2013).

Georgia: Information on the distribution of American eel in Georgia has been collected since 2004 and these data have been mapped as part of the Fishes of Georgia project (Straight *et al*. 2009, entire). American eel are most abundant in south Atlantic slope drainages which are largely undammed (figure 18). Coastal watersheds in Gulf of Mexico drainages also contain American eels, but at lower density than Atlantic slope drainages. Based on the distribution maps, American eels occur in the Chattahoochee, Flint, Ochlockonee, Suwannee, Satilla, Ocmulgee, Oconee, Altamaha, Ogeechee, and Savannah River Basins. Records only include known occurrences rather than a full distribution based on known and potential occurrences (Straight *et al*. 2009, entire).
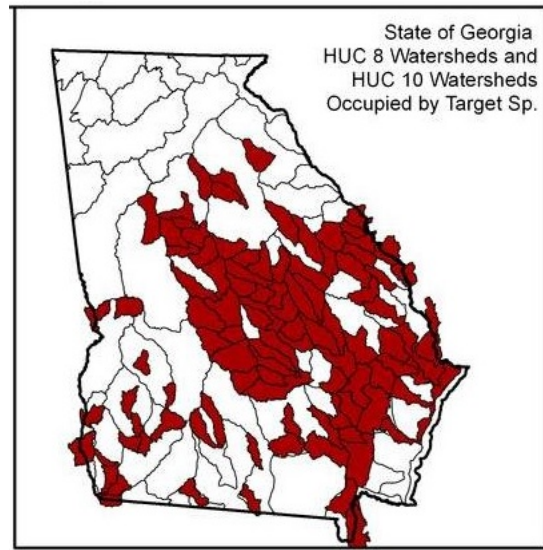
FIGURE 18—American eel distribution in Georgia. (http://fishesofgeorgia.uga.edu)

This method underestimates the species' distribution, and does not make any assumptions about watersheds where a record does not occur. It also helps identify watersheds where additional sampling may be needed. These mapped distributions include some older records of the species and may not reflect current distribution. Current distributions may be smaller due to historical records being included or may be larger due to either range expansions or limitations of the data (lack of records).

Florida: American eel are widely distributed on the east and west coasts of Florida. Peak landings in the 1970s and 1980s, including small harvests on the west coast, exceeded 100 tons (figure 10). The harvest declined in the late 1990s (figure 19). Although the number of permits has increased recently, the total harvest and mean catch per permit have been relatively stable (figure 19).
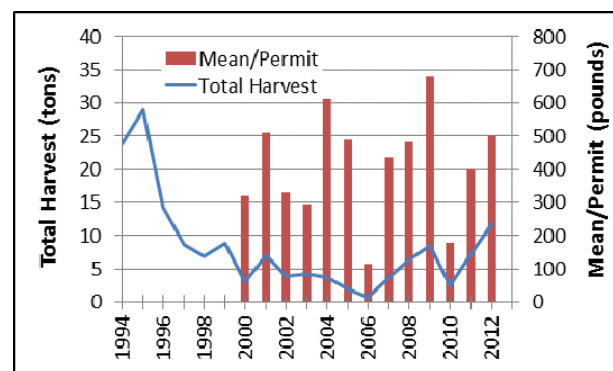
FIGURE 19—Florida eel harvests 1994–2012 (data from Florida Fish and Wildlife Conservation Comm.).

5.5   GULF OF MEXICO

American eels occur throughout the Gulf of Mexico, including extensive distances inland along many large tributaries (Lee *et al*. 1980, pp. 59–60). Along the U.S. Gulf Coast, eel density is generally low and commercial eel fishery landings are very small (figure 10).

Texas: American eels were originally found in large rivers from the Red River to the Rio Grande but have been extirpated in several drainages, as a result of dams that impede upstream migration (Hendrickson and Cohen 2012, p. 1; Thomas *et al*. 2007, p. 2; Hubbs *et al*. 1991). Texas records from the early 20th century are scarce. The Smithsonian National Museum of Natural History online database (http://collections.nmnh.si.edu/search/fishes/) shows only three specimens, one from the mouth of the Rio Bravo in 1858 (the holotype); one from Galveston Bay in 1935; and a third collected at Compano Bay Beach in 1940.

The current abundance and distribution of American eel in Texas coastal and inland waters is not well documented. American eels appear to be rare in inland waters (Mike Ray, Texas Parks and Wildlife Department (TPWD), personal communication, 2005), although sampling generally does not target eels. Notable abundances have been documented downstream of some dams on Texas rivers where sampling has targeted eels (SRA 2009 and ETEC 2010). Eels are abundant in the Lower Trinity River downstream of Lake Livingston dam (SRA 2011; ETEC 2010), and in the lower Sabine River where FERC relicensing of the Toledo Bend Project has allowed the Service to prescribe upstream and downstream eel passage at the first dam on the river (USFWS 2012, pp. 11–18).

American eel are present, but uncommon in many coastal Texas waters (Thomas *et al*.2007, entire). In the last 30 years, the TPWD has documented eels in Matagorda/San Antonio Bays (2 in the 1980s, 10 in the 1990s, and 3 in 2003), Corpus Christi Bay (in 1984 to 2001) and Lake Anahuac (Mike Ray, personal communication, 2005). Warren *et al*. (2000 in Thomas *et al*. 2007, p. 1–2) list the following drainage units for distribution of American eel in the State; Red River (from the mouth upstream to and including the Kiamichi River), Sabine Lake (including minor coastal drainages west to Galveston Bay), Galveston Bay (including minor coastal drainages west to mouth of Brazos River), Brazos River, Colorado River, San Antonio Bay (including minor coastal drainages west of mouth of Colorado River to mouth of Nueces River), Nueces River. Hubbs (2002) reported that dams have precluded young eels from repopulating Caddo Lake in northeast Texas.

Louisiana: Eels are commonly found among backwater fish communities within lakes, oxbows, and impoundments present in large river floodplains of Louisiana and there is a small commercial fishery in these areas (Ross 2001). Eels are particularly abundant in the Pearl River and estuary. Several thousand American eels were recently encountered in a fish kill survey of the lower Pearl River along the Louisiana-Mississippi border (LDWF 2011). Hundreds of eels were reported in a fishery study conducted in an adjacent Louisiana estuary (LDWF 1982).

Alabama: American eels have been collected from every river system of the Mobile basin, as well as from coastal drainages in southeastern Alabama, from the Apalachicola drainage west to the Escatawpa River system (Mettee *et al*. 1996, p. 110; Boschung and Mayden 2004). They are common in the Alabama River and the Alabama Division of Wildlife and

Fisheries has caught eels in upstream tributary rivers to Jordan Dam on the Coosa River and in Holt Reservoir in the Black Warrior River (unpublished data from S. Chance, U.S. Fish and Wildlife Service, 15 Jan 2014). American eels are most numerous in the southern part of Alabama, particularly in the Mobile Delta (Mettee *et al*. 1996, p. 110). They are also found in low numbers throughout the Tennessee River in northern Alabama (A. Henderson, Tennessee Valley Authority, personal communication, 20 Dec 2013). American eels are probably more common in Alabama waters than their numbers in surveys and museum collections indicate (Boschung and Mayden 2004).

Mississippi: In Mississippi (Ross 2001), American eels are widespread in the Gulf of Mexico basin (streams that flow into the Gulf of Mexico rather than into the Mississippi River). Records of the Mississippi Museum of Natural Science (MMNS) include eels captured in coastal rivers such as the Pascagoula, Pearl, and Tombigbee Rivers although few specimens are in the collection (M. Roberts, MMNS, personal communication, 12/19/2013). In the Bogue Chitto River in Mississippi and Louisiana, American eels are rare or at least seldom captured (Stewart *et al*. 2005). Electrofishing in coastal rivers and elsewhere occasionally yields single captures of American eels in Mississippi, where the species seems to have a wide riverine distribution but is not commonly encountered anywhere (Dennis Riecke, personal communication, 2005). Sampling by Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) biologists of such aquatic habitats in Mississippi is very limited; the State does not have a routine stream sampling program (Dennis Riecke, MDWFP, personal communication, 2005).

Colorado: The map in Lee *et al*. (1980, p. 60) indicates no eel occurrences in Colorado, but American eels have been reported from the Rio Grande in Colorado. Referring to Colorado, Lynch (in Everhart and Seaman 1971) stated that "historical records indicate that the American eel was once common to the Rio Grande and Arkansas River drainages." Fuller *et al*. (1999, p. 37) indicated only aquaculture occurrences of American eels in Colorado and specifically described a record of eels that escaped from an aquaculture facility in Conejos County, Colorado in the San Luis Valley (Rio Grande drainage).

New Mexico: Sublette *et al*. (1990) describe the historical presence of American eel in New Mexico as occurring in the Rio Grande and Pecos River drainages, and probably also the Canadian River. Although eels were believed to have been extirpated in New Mexico, they were found in the lower Rio Grande and Chama River, presumably from an aquaculture facility in Colorado (Sublette *et al*. 1990), but possibly from downstream waters.

5.6 MISSISSIPPI RIVER BASIN

The American eel persists in a portion of the historical range of the Mississippi watershed, including the major tributaries the Missouri, Arkansas, Ohio, and Tennessee Rivers, although some headwater locations are blocked by impassable dams, and abundance in

many areas has declined during the past half century (Becker 1983, p. 258). The distribution of the American eel remains widespread in the Mississippi watershed, despite the construction of many dams, such as the series of 27 navigation locks and dams between St. Louis, Missouri and Minneapolis, Minnesota. These navigation locks and dams were built to hold back water and form deeper navigation pools while allowing for barge passage through the locks. Presumably, these lock and dam complexes allow for eel passage when barges pass or eels pass during high water stages, as American eel are still found above Keokuk Dam (Iowa) today. Despite these (and many other) dams, American eel are found as far as St. Cloud, Minnesota upstream of 30 dams in the upper Mississippi River (Delphy, 2013, p. 1). However, eel abundance in the Upper Mississippi River declined between 1992 and 2010 (figure 20) (Phelps *et al*. 2014, p. 168).
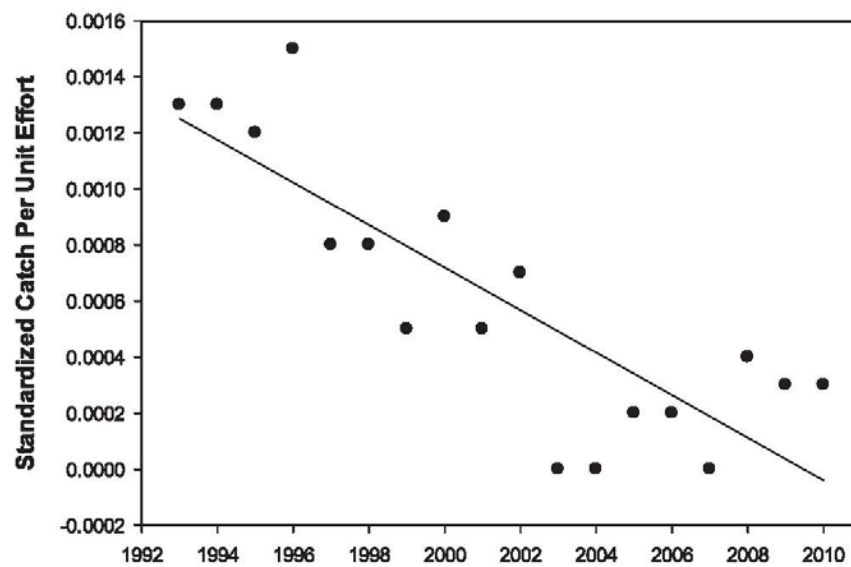
FIGURE 20— Standardized catch per unit effort of American eels captured in the Upper Mississippi River from 1993 to 2010. Capture types included electrofishing, fyke nets and hoop nets. From Phelps *et al*. 2014, p. 168.

Kentucky: According to a report by Kentucky Department of Fish and Wildlife Resources (KDFWR) (Thomas 2013), the KDFWR fish collection database includes a total of 91 American eel records from 1877 to 2013 (Thomas 2013). Although these records were obtained from various sources (e.g., early ichthyological surveys, angler reports, and scientific collecting permit data), nearly 75 percent were from KDFWR stream surveys. In many cases, eels were captured incidentally during sportfish sampling, which usually involved boat electrofishing; they have been captured occasionally by anglers and less often taken in wadeable habitats using seines or backpack electrofishing. Additional information

(i.e., specimen data) on eels captured is largely unavailable. Most records are represented by a single individual that was released upon capture.

In general, fewer than 10 American eel records have been reported per decade in Kentucky since 1950. The 15 available records prior to 1950 include collections from the late 1800s (e.g., Jordan and Brayton 1878 <u>in</u> Thomas 2013; Woolman 1892 <u>in</u> Thomas 2013) and early to mid-1900s (e.g., Welter 1938 <u>in</u> Thomas 2013; Clark 1941 <u>in</u> Thomas 2013). The disproportionately large number of records during the 1980s resulted mostly from intensive fish surveys in the Kentucky and Green River drainages during 1982 to 1985 by KDFWR using boat electrofishing. Since 2010, nine records have been reported, six of which were from the upper Green River drainage.

<u>Tennessee</u>: Eels are present in Tennessee waters of the Mississippi River and are occasionally caught during Tennessee Wildlife Resources Agency (TWRA) fisheries surveys (W. Reeves, TWRA, unpublished data). According to Etnier and Starnes (1993, p. 120), eels are uncommon in Tennessee waters but are still occasionally taken in direct tributaries to the Mississippi River and in the Cumberland and Tennessee rivers as far upstream as Dale Hollow Reservoir and Knoxville, respectively. The Tennessee Valley Authority (TVA) also reports that eels are present throughout the Tennessee River to the Knoxville area, about 1,050 km (650 mi) upstream of the confluence with the Mississippi River (A. Henderson, TVA, personal communication). These eels presumably move upstream through lock facilities, since no dedicated eel passage exists at the Tennessee River dams. The American eel appears on Tennessee's list of Species in Need of Management (Starnes and Etnier, 1980)—a category of the Tennessee Natural Heritage Inventory Program that denotes a species in need of information on species distribution, habitat needs, limiting factors, and other biological and ecological data.

<u>Iowa:</u> Eels are occasionally encountered during electrofishing surveys of the Mississippi River. Five eels measuring 432 to 533 mm (17 to 21 in) have been caught in Pool 16 of the Mississippi River since 2007 (A. Thiese, Iowa Department of Natural Resources, personal communication, 12/30/2013).

<u>Arkansas:</u> Robison and Buchanan (1988, pp. 101–103) reported eel presence in all of the major Arkansas watersheds: the Arkansas, White, Ouachita, Red and St. Francis Rivers, as well as the Mississippi River. The authors noted that eels were present to the headwaters of these rivers, although not abundant due to the presence of numerous dams. Eels were most abundant in the lower Arkansas and White rivers. Eel are found in the White River to headwaters such as the Current River in Missouri. Cox *et al*. (2014, entire) studied eel demographics in the Ouachita River basin and eel migration from the White River into the Arkansas River Navigation System and collected 264 eels (doubling the number of eels previously collected in Arkansas). They documented high concentrations of small eels below dams in both rivers, concluding that upstream migration was impeded by the dams.

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Missouri River: Eels are found in the Missouri River and many of tributaries in the States of Missouri, Iowa and Nebraska as far upstream as the Gavins Falls Dam in Yankton, South Dakota. In Missouri, eel capture records also include Osage and Gasconade Rivers, both tributary to the Missouri River, as well as the Meramec River, a tributary of the Mississippi River.

Kansas: Haslouer *et al.* (2005, p. 35) describe the status of American eel in Kansas. Formerly ranging nearly statewide as migrants from the Gulf of Mexico, the last catalogued specimen of an American eel from Kansas in the Kansas University collection is from 1979. Cross and Collins (1995 in Haslouer *et al.* 2005, p. 35) also noted a non-vouchered specimen taken in the Kansas River in 1987. Dams and flow diversions have rendered a good deal of the formerly documented range of this species inaccessible and the Kansas Natural History Inventory lists this species as "imperiled" in Kansas (Haslouer *et al.* 2005, p. 35) and the authors recommend that it be State listed as endangered.

Minnesota: The historical distribution of American eel in Minnesota was likely restricted to the St. Croix River and the Mississippi River downstream of St. Anthony Falls, Minnesota. However, since the construction of the lower and upper St. Anthony locks for commercial navigation, occurrences in the Mississippi upstream to St. Cloud, upstream of 29 Mississippi River dams, have been confirmed from angler and newspaper photographs including a former Department of Natural Resources' State record caught in the Crow River. The occurrences of American eel in the Lake Superior drainage (i.e., Duluth-Superior Harbor and Blackhoof and Knife rivers) likely followed the construction of the Welland Canal bypassing Niagara Falls, or possibly via the Chicago Sanitary and Ship Canal that connects the Mississippi Drainage to the Great Lakes (Hatch *et al.* in Delphy 2013, p. 1).

Although survey and angling effort is not uniform through time, records from Minnesota waters have declined (figure 20). From 1971 to 1980, there are 35 records, 1981 to 1990 (25), 1991 to 2000 (39) and 2001 to 2012 (13) (Hatch *et al.* in Delphy 2013, p. 1). According to NatureServe (2013), the American eel is considered critically imperiled in Ontario and South Dakota, imperiled in Wisconsin, vulnerable in Iowa, and a special concern species in Minnesota.

Ohio: Voucher specimens and field collection records of the Ohio State University Museum of Biodiversity (OSUMB) include 94 American eel from Ohio waters (B. Zimmerman, OSUMB, personal communication, Dec. 12, 2013). These eels were collected in the Ohio River and tributary streams as well as Lake Erie and tributaries. The records date from the 1960s (15), 1970s (43), 1980s (14), 1990s (8) and only 2 eels since 2000.

5.7 CANADA

The American eel is widespread in the provinces of eastern Canada northward to the English River, Labrador (Wildlife Division 2010, p.11). The abundance and distribution in Canada has declined, particularly in the upper St. Lawrence River and Lake Ontario (SLR/LO). According to COSEWIC (2012, p. v), estimated changes in abundance indices from the 1950s to the 2000s (roughly three generations of American eel) were +7.1 to -96.2 percent within the western portion of the species' range, while trends were mixed within the eastern portion of Canada. In particular, abundance indicators for the SLR/LO stock declined by as much as 99 percent over about two decades (figure 21), and four out of five eel abundance time series from the lower St. Lawrence River and Gulf of St. Lawrence have also declined. However, trends in abundance in other areas are highly variable (SARA 2012)—during the same 30-year period that eel stocks declined in the upper SLR/LO, some eel abundance indices in coastal waters of the Gulf of St. Lawrence tripled (Bernatchez *et al*. 2011, p. 1).
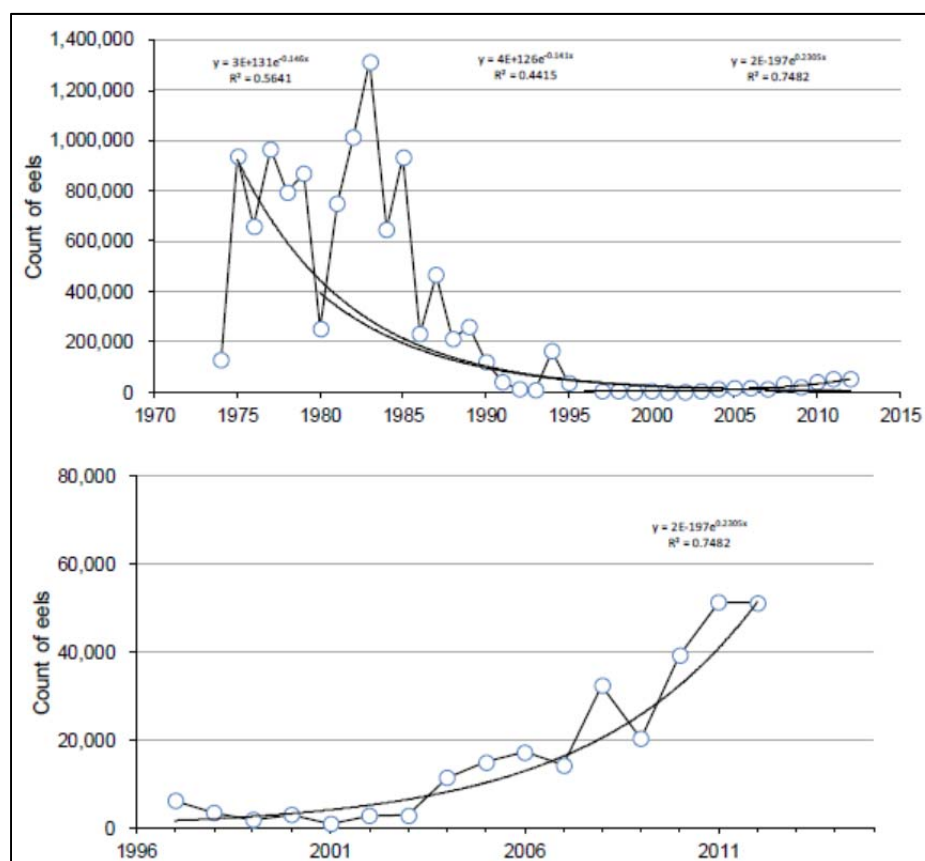

FIGURE 21—Juvenile American eel abundance and trend analyses at the Moses Saunders Dam eel ladders, 1974–2012. The upper panel shows the full series and the lower panel shows data for 1997–2012. Trend analyses exclude the first year of operation in 1974 and the 1996 data are missing (from Cairns *et al*. 2014, p. 117).

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The COSEWIC (2012, p. v) summarizes the eel population sizes and trends in Canada, as described below. Indices of abundance based on fishery landings indicated negative change. Abundance relative to the 1980s is very low for Lake Ontario and St. Lawrence River fish according to fisheries-independent data. Between 1996 and 2010, estimates of the total number of maturing eels declined by 65% in the Great Lakes and upper St. Lawrence River area, despite the reduction in mortality from commercial fisheries (50 percent of fishing effort between 2002 to 2009). An index of year class strength indicated a substantial decline of juvenile eels migrating upstream in the Sud-Ouest River (lower St. Lawrence River) between 1999 and 2005. Trends in some areas (e.g., New Brunswick) were mixed while areas such as Newfoundland and southwest Nova Scotia indicated some declines between the 1980s and the 2000s. Currently, where eels continue to persist in inland rivers and lakes in Canada, their abundance is now very low, and eels are approaching extirpation from all inland watersheds in Ontario (MacGregor *et al.*, 2008, pp. 362–364). In eastern portions of Canada, American eel are still widespread, although indices of abundance appear to be variable (COSEWIC 2012, pp. 33, 59).

5.8   CARIBBEAN, CENTRAL AMERICA AND SOUTH AMERICA

Some American eel leptocephali are carried into the Caribbean Sea by marine currents (Kleckner and McCleave 1985). Benchetrit and McCleave (2015, pp. 9–10) found that the American eel distribution includes Caribbean Sea islands with permanent rivers, Central America, Colombia, Venezuela west of the Orinoco River, and northern Trinidad (figure 1). The authors concluded that eels are not found further east or south due to the presence of the Brazil current which inhibits larval transport south of Trinidad. Yellow eels are found in freshwater streams in the Greater Antilles and some other Caribbean Islands (Crain *et al.* 2011), the Caribbean coasts of Central and South America (McLarney *et al.* 2010), including all of the Atlantic basins of Costa Rica (Angula *et al.* 2013). An assessment of low-head dam effects on distribution of fishes in Puerto Rico found American eels at 57 of 118 sample sites (Cooney and Kwak 2013, p. 181). Kwak *et al.* (2007, p. 87) found American eels in Puerto Rico at 32 of 81 sites sampled— abundance was similar across seasons and sites, although the distribution within watersheds was limited by barriers. There were 1 to 16 eels per site, ranging from 132 to 885 mm (5 to 35 in), a mean density 62.0 eel/ha (25.1/acre), and mean biomass of 27.4 kg/ha (24.5 lb/acre) (Kwak *et al.* 2007, p. 87). Diaz (2014 entire) noted that information on eel distribution and abundance in Mexico is scarce—eels are present in the northernmost Gulf state of Tamaulipas (but probably extirpated from the Rio Bravo), and eels are present in the southern states of Tabasco, Chiapas, Yucatán, and Quintana Roo.

Landings data for the Caribbean Basin and the Gulf of Mexico are available from the United Nations Food and Agricultural Organization (FAO) from 1950 onwards (Cairns *et al.* 2014 p. 54). The FAO summary data report eel landings in the Caribbean Basin and Gulf of

Mexico from only Cuba, the Dominican Republic and Mexico. Reported landings from Cuba have never exceeded 2,000 lb per year while reported landings in the Dominican Republic and Mexico have been highly variable. Reported landings reached their maximum values in both countries in 2011, with the Dominican Republic reporting 72 tons and Mexico reporting 140 tons. Crook and Nakamura (2013, p. 26) report a glass eel fishery in the Dominican Republic, but provide no harvest data. There is a glass eel fishery in Haiti and the harvest may be 4 to 5 tons annually (J. McCleave, personal communication, 22 Oct 2014).

5.9 SUMMARY

The status and abundance information described above are based upon reported commercial landings, research surveys (e.g., netting, electrofishing, etc.), fishway monitoring, and presence/absence data reported from museum collections, recreational catches, and other sources. Different sources of data (presence/absence, harvest summaries, YOY abundance indices, and/or habitat studies) were available for each region and no data were provided for some states. Differences in data type, source, and periods of record preclude quantitative comparisons among regions and standardized analyses of trends in abundance. The available data sources provide presence/absence data that demonstrate that American eel remain in most of their historical range and have been introduced in some new areas through canals, locks and fishways.

The types of abundance data described above are of very limited value for characterizing abundance trends or exploring factors influencing those trends (Haro *et al*. 2000, p. 14). Very few data sets have been collected with systematic, repeatable methods that produce standardized results over long periods of time. Data on landings and fishing effort are known to be incomplete or nonexistent, and there is the possibility that catches are underreported. Even when landings data are accurate, market conditions, economic opportunities for commercial fishers, and fishing regulations have significant effects on eel landings that are independent of eel population abundance. The extensive harvest of young yellow-phase eels for use as crab bait in the Chesapeake Bay region and as live bait for recreational fisheries for species such as striped bass (*Morone saxatilis*) in the Mid-Atlantic region to New England are additional sources of landings that may be underreported (EPRI 1999). A further complication is that fisheries for American eel target many life stages, from glass eels and elvers to the sexually mature silver-phase stage, yet the size and age composition of reported landings is, for the most part, undocumented. Effort data are often lacking, so harvests cannot be standardized as catch per unit effort. As a result of these various issues, the contribution to annual harvests of individual year classes of a species that can be exploited from ages 1 through more than 20 is not known. The ASMFC is currently working to encourage states to implement whole life stage surveys, but it is unclear when any might be implemented and completing these studies will take decades to complete.

6   STRESSORS

6.1   CLIMATE CHANGE

The increasing atmospheric concentration of greenhouse gases has caused the global average air temperature to rise steadily for decades, particularly since the 1950s (Intergovernmental Panel on Climate Change (IPCC) 2013 p. 4). The first decade of the 21st century has proven to be the hottest decade since scientists began recording global temperatures in the 1880s, with the 1990s following close on its heels as the second hottest decade (IPCC 2013 p. 5). With respect to fish, climate warming has been implicated in short-term phenotypic changes of traits of diadromous and marine fish species, including age at maturity, age at juvenile migration, growth, survival, fecundity, and the timing of reproduction (Crozier and Hutchings 2014, p. 70).

Sea surface temperatures in the Sargasso Sea have been rising for more than three decades (figure 22) (Bonhommeau *et al.* 2008, p. 75). Rising ocean temperatures have significant implications for eel spawning habitat in the Sargasso Sea, and may be affecting American eel migration or aggregation for spawning.   Climate induced changes to marine and freshwater habitats may impact American eel by changing the characteristics of thermal fronts in Sargasso Sea spawning sites, altering the currents that carry larvae to continental rearing areas, or changing the biological productivity that affects food availability, particularly to larvae (Friedland *et al.* 2007, p. 519; Bonhommeau *et al.* 2008, p. 77; Miller *et al.* 2009, p. 235–238). These issues are described in the following sections.
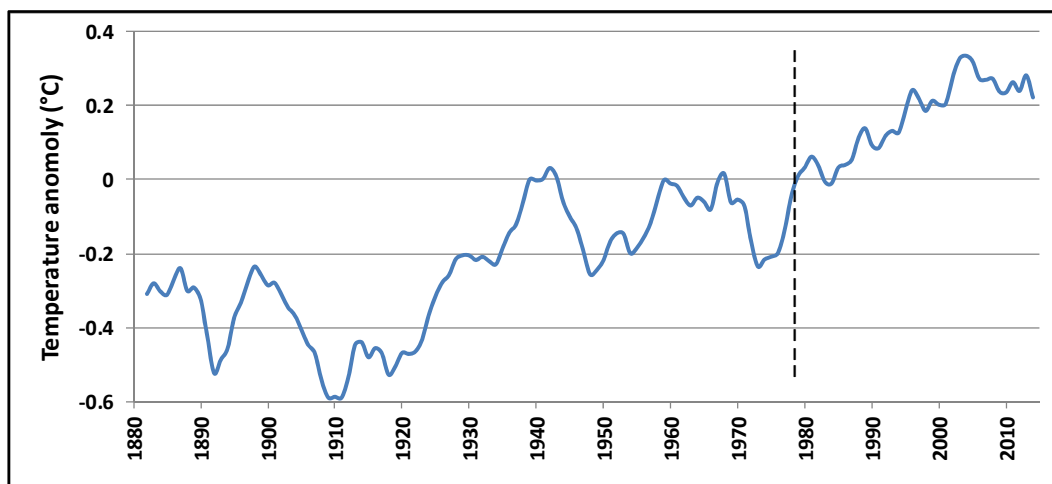
FIGURE 22—Annual average Atlantic Ocean sea surface temperature anomaly (5-year moving averages) from 1880 to 2014 at 0°N to 30°N (data from *ftp://ftp.ncdc.noaa.gov*). Dashed line indicates the onset of the positive regime shift in sea surface water temperature described by Bonhommeau *et al.* (2008, p. 75).

6.1.1 OCEAN WARMING

With respect to ocean warming that may affect American eel migration and spawning, the IPCC (2014, p. 4) summary noted that, "Ocean warming dominates the increase in energy stored in the climate system, accounting for more than 90% of the energy accumulated between 1971 and 2010 (high confidence), with only about 1% stored in the atmosphere. On a global scale, the ocean warming is largest near the surface, and the upper 75 m warmed by 0.11 [0.09 to 0.13] °C per decade over the period 1971 to 2010." The warm, high salinity waters of the southwestern Sargasso Sea are the only known habitat where American eel can successfully spawn (see sections 3.1 and 4.1). Studies of American, European, and Japanese eel have found inverse correlations between recruitment and sea surface temperature in mid-ocean spawning areas (Bonhommeau et al. 2008, pp. 76)—a 28 year time series of American eel glass eel abundance was inversely correlated with Sargasso Sea surface temperatures (figure 23). Similar inverse correlations were documented for European and Japanese eel using 46 and 36 years of data, respectively (Bonhommeau *et al*. 2008, pp. 74–78; Knights 2003, p. 237). The authors concluded that climate warming of the Sargasso Sea inhibits spring thermocline mixing and nutrient circulation, with negative impacts on productivity, and hence food availability for larval eels.
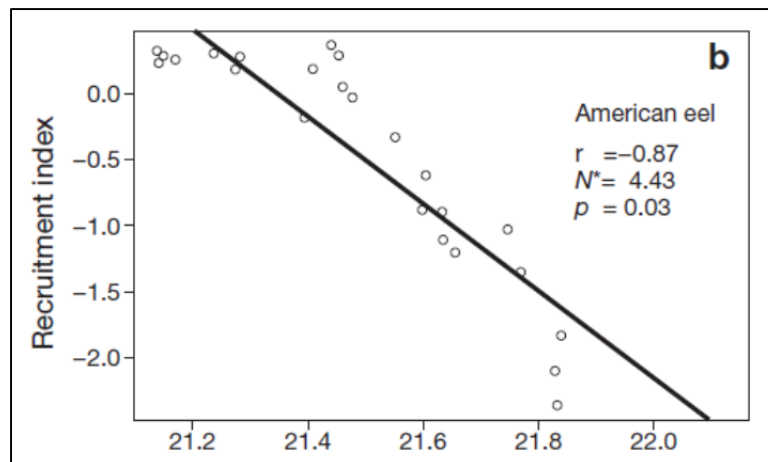
FIGURE 23—Long-term relationship (5-year moving averages) between the Sargasso Sea surface temperature (x-axis in °C) and American eel recruitment indices, lagged by 1.5 year to account for migration duration (from Bonhommeau *et al*. 2008, p. 76). Recruitment index data are glass eel abundance at Little Egg Inlet, New Jersey and Beaufort Inlet, North Carolina.

Sampling of American and European eel larvae in the Sargasso Sea indicate that spawning locations vary from year to year, but American eel spawn further west than European eel with some overlap of the two species. A northward shift of the 22.5°C (72.5°F) isotherm in the Sargasso Sea spawning area is correlated with a decrease in European glass eel

abundance (Friedland *et al.* 2007, p. 523), possibly by shifting eel the spawning location northward to areas with unsuitable spawning conditions. Durif *et al.* (2011, p. 464) found that European glass eel abundance in the Skagerrak coastal area of Norway was inversely correlated with Sargasso Sea surface temperatures. Knights (2003, p. 237, 240) postulated that high temperatures in the Sargasso Sea were related to gyre spin-up that affects major ocean currents, slows the migration of eel larvae, and results in increased losses from starvation and predation.

Although American eel larvae have a much shorter migration distance than European larvae, warming of the North Atlantic Ocean may affect American eel spawning success or larval survival. Models of the North Atlantic climate predict that the Gulf Stream will shift northward and slow in response to warming and increased stratification (Hare *et al.* 2014, p. 2). In summary, American eel recruitment is correlated with Sargasso Sea temperatures, the position of thermal fronts, and possibly thermal stratification in spawning areas and ocean currents. The relationship between these physical oceanographic process and climate change remains speculative. Further research is needed to assess the causal relationship between American eel glass eel recruitment and Sargasso Sea temperatures.

6.1.2   THE NORTH ATLANTIC OSCILLATION

The North Atlantic Oscillation (NAO) is an index of natural fluctuations in the relative strength of the atmospheric pressure systems measured at Iceland and the Azores, which are typically low and high pressure weather systems, respectively. An increased NAO index corresponds to greater pressure differential between these systems and strong westerly winds which affect heat transfer and ocean circulation (e.g., tempering the climates of northern Europe during periods of high NAO). The Gulf Stream and North Atlantic Current both gradually weakened during the low NAO period of the 1960s and then intensified in the subsequent 25 years of persistently high NAO to a record peak in the 1990s (Curry and McCartney 2001, p. 3374). Thus, the NAO is not a measure of marine habitat conditions, per se, but indicates the strength of the atmospheric pump that drives North Atlantic heat transfer and affects ocean circulation.

The NAO is correlated with a wide variety of biological measures, including the survival and recruitment of American and European eel. The NAO may affect eel recruitment by 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 far to the south in the Sargasso Sea (Friedland *et al.* 2007, pp. 524–527; Bonhommeau *et al.* 2008, p. 78; Miller *et al.* 2009, p. 244). Miller (2014b, entire) hypothesizes that the NAO may affect the production of marine snow, an important food source of small eel larvae, which could result in density-dependent survival of eel larvae at the time of first feeding.

American eel spawner abundance and larval recruitment are inversely correlated with the NAO. That is, years with high NAO are associated with low spawner abundance and low survival of Atlantic eel larvae (Bonhommeau *et al.* 2008, p. 78; Cairns *et al.* 2014, p. 6). The NAO variability during positive phases is correlated with American eel allelic richness and with the effective number of breeders (similar to N_e, Section 2.3) (Côté *et al.* 2013, pp. 1771–1773). One of the longest fisheries-independent American eel abundance indices, beginning in 1952 on the Miramichi River, New Brunswick, is based on annual electrofishing surveys at 15 to 70 sites (Cairns *et al.* 2014, p. 15). The Miramichi eel index and the winter (December to March) NAO index are strongly correlated (figure 24) (Cairns *et al.* 2014, p. 6). The authors stated that the correlation suggests a link between climate and oceanography that could affect recruitment of American eels to continental waters. A similar relationship was documented for yellow eels captured at the Moses-Saunders Dam, St. Lawrence River eel fishway, where the abundance of yellow eels was correlated with the NAO (ICES 2001).

Knights (2003, p. 238) notes that some authors argue that sea surface temperature differences in the North Atlantic are the main drivers of the NAO and associated continental climate change. For example, Rodwell *et al.* (1999 in Knights 2003, p. 238) suggest that Gulf Stream heat transfers between the sub-tropical gyre and the sub-polar gyre south of Greenland force the NAO. If true, then ocean temperature dynamics may be the underlying environmental driver of larval eel abundance. It is possible that variation in the strength and
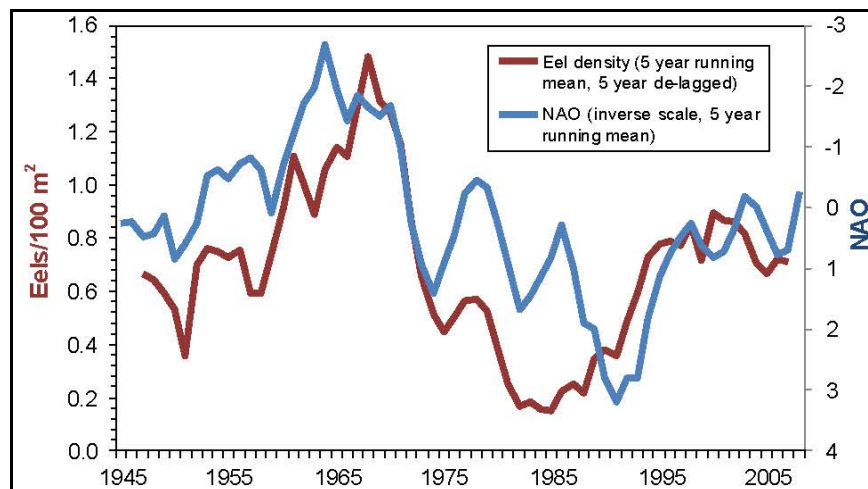
FIGURE 24—Inverse relationship between Miramichi River eel density and the winter (December to March) North Atlantic Oscillation index (shown as reverse scale). Data are 5 year running means and eel density is de-lagged by 5 years to account for the mean age of juvenile eels. The correlation coefficient is -0.71 and the degrees of freedom were adjusted to account for autocorrelation (from Cairns *et al.* 2014, pp. 6, 92).

volume of the ocean currents that transport larval eels, as indicated by changes in the NAO, are responsible for the correlations with the subsequent abundance of glass eels.

Like American eel, long-term European eel glass eel abundance indices are inversely correlated with the NAO (Knights 2003, p. 237; Friedland *et al.* 2007, p. 219; Kettle *et al.* 2008, p. 1; Miller *et al.* 2009, p. 231; Durif *et al.* 2011, p. 464). Although the NAO index has declined since the late 1990s, no overall improving trend in European glass eel recruitment was noted during this period (ICES 2012). With regard to European eel larvae, increased current velocity in the North Atlantic during high NAO may send larvae into the subpolar gyre before they are ready to metamorphose and settle, resulting in low recruitment in the northern part of the distribution area for these years (Durif *et al*. 2011, p. 470).

6.1.3 PALEOCLIMATIC PERSPECTIVE

The timing of the evolutionary divergence of American and European eel indicates that speciation may have occurred about 2.6 million years ago as a result of onset of Pleistocene climate cooling (see Section 2.1). During the Pleistocene, the two Atlantic eel species adapted to at least five successive glacial/inter-glacial periods—likely shifting their continental distributions, marine migration routes, and ocean spawning locations in response to changing climate conditions. The most recent glacial epoch was the Wisconsinian glaciation, with the maximum glacial extent occurring about 22,000 years before the present.

The characteristics of Pleistocene climates are captured in many types of evidence, such as ice cores, sediment records, glacial deposits, and fossils. With regard to the Wisconsinian glacial maximum, data show that glacial conditions: (1) inhibited North Atlantic surface water circulation for thousands of years due to a decrease in North Atlantic air temperature by 15°C (59°F); (2) decreased North Atlantic water temperature by about 2°C (3°F), and; (3) decreased surface water salinity by 2 to 3 ppt (Keffer *et al*. 1988 pp. 440–442; Cortijo *et al*. 1998, pp. 40–42). These changes had a direct impact on general North Atlantic circulation by shifting sub-polar waters southward to Gibraltar, inhibiting the speed of the Gulf Stream, reducing the strength of the North Atlantic drift, and moving the gyre boundary and associated currents farther to the south (Keffer *et al*. 1988 pp. 440–442; Lecomte-Finiger 2003, p. 274). These oceanic climate changes likely reduced the reproductive success of American eel and could account for the contemporaneous decrease in N_e described in section 2.3.

The most recent deglaciation occurred about 10,000 to 12,000 years before the present and made North Atlantic environments unstable in response to large inputs of glacial meltwater and rapid changes in air temperature. During the Wisconsinian deglaciation, American eels likely experienced repeated sudden changes in thermohaline overturn, repeated surface temperature changes of more than 5°C (7°F) in fewer than 40 years, and large shifts in the

poleward flow of warm Atlantic surface waters over decadal time frames (Lehman and Keigwin 1992, pp. 757, 762). American eel may have experienced similar climate changes during the previous Pleistocene deglaciation events.

Wirth and Bernatchez (2003, p. 686) documented a two orders of magnitude decline in American eel N_e (i.e., evidence of a population bottleneck), the timing of which corresponds to the glacial maximum of the Wisconsinian glaciation. Wirth and Bernatchez (2003, p. 687) provide a cautionary note for future eel management, "(The) lessons learned from the past suggest that climatic changes that affect the Gulf Stream have an intricate effect on catadromous fishes". If climate warming changes the thermal characteristics of the eel spawning grounds, or affects the ocean currents that disperse eel larvae, then future the American eel abundance may be affected.

6.1.4 SUMMARY

Changes in the abundance and recruitment of young eels are correlated with sub-tropical ocean temperature conditions and changes in the NAO. This is true for American and European eels. North Atlantic Ocean circulation, such as the strength of the Gulf Stream, is also changing in response to climate change. However, the available research documents only indirect correlations between ocean circulation and eel abundance.

American eel larval survival may be reduced by climate induced warming of the North Atlantic. This could happen if climate change: (1) increases the water temperature of spawning habitats in the Sargasso Sea; (2) shifts eel spawning areas northward, as measured by the position of the 22.5°C isotherm; and/or (3) reduces nutrient upwelling and primary productivity in response to increased thermal stratification. Correlations of Atlantic and European eel abundance with the NAO demonstrate that broad-scale physical oceanographic process may affect Atlantic eel abundance. However, the research to date has not positively identified the specific processes that are affecting American eel abundance.

In summary, climate change is affecting ocean currents and shifting the location of Sargasso Sea habitats with the thermal characteristics associated with Atlantic eel spawning. Climate mediated changes to marine habitats may affect eel recruitment by 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 in the Sargasso Sea. These climate changes are also correlated with the decline of European eel. Indeed, Baltazar-Soares, *et al.* (2014, p. 104) conclude that "…regional atmospherically driven ocean current variations in the Sargasso Sea were the major driver of the onset of the sharp decline of European eel in the 1980s."

6.2 PARASITES

Anguillid eels can be parasitized by freshwater species of Myxozoa, Monogenea, Cestoda, Nematoda, and Acanthocephala (Gerard *et al.* 2013, p. 1) with an estimated total of 63 known eel parasite species among these classes (Kennedy 2007, p. 320). These parasites are freshwater species that cannot tolerate full salinity, and thus, they cannot be acquired in fully marine environments by larvae or silver eels, but are transferred among hosts in brackish or freshwater habitats (Lecomte-Finiger 2003, p. 270). Most of these parasites are native and have co-evolved with their eel primary hosts, and the majority (86 to 95 percent, depending upon the species of eel) are harmless or cause only very local tissue damage (Kennedy 2007, p. 320). Parasite life cycles may be complex—transmission in more than 63 percent of the traditional host-parasite relationships requires at least one intermediate planktonic host, often a prey item such as a copepod (Kennedy 1992, <u>in</u> Lecomte-Finiger 2003).

Three exotic eel parasites have been described in the Americas, *Anguillicoloides crassus* (previously *Anguillicola*), *Pseudodactylogyrus anguillae* and *P. bini*, (Barse and Secor 1999, p. 7). These three exotic parasites are known to cause significant damage to American eels when the parasites are present in large numbers in optimal growth and transmission conditions such as crowded eel aquaculture facilities (Kennedy 2007, p. 319). The following sections describe the history of the introduction and spread of these parasites through the Americas and their effects upon American eel in experimental and natural settings.

6.2.1 ANGUILLICOLOIDES CRASSUS

Parasitic nematodes in the genus *Anguillicoloides* are native to the Indo-Pacific where each species has a host relationship primarily with a single species of eel (Laetsch *et al.* 2012, pp. 11–12). In their original setting, nematodes of this genus cause no apparent outward damage, despite the fact that adults of all *Anguillicoloides* spp. live in the lumen of the swimbladder (the buoyancy control organ) and feed on blood (Szekely *et al.* 2009, p. 202). The parasite of concern for American eel is *A. crassus*, a highly infectious exotic nematode that infects the swimbladder of Anguillid eels. The Japanese eel, *Anguilla japonica* is the traditional host of *A. crassus* (Laetsch *et al.* 2012, pp. 11–12). Infected Japanese eel do not show the inflammation and pathological changes of the swim bladder that are seen in American eel, even in the crowded stressful conditions found in Japanese and Taiwanese eel farms (Barse and Secor 1999, p. 9).

The life cycle of *Anguillicoloides crassus* and the host relationship with American eel are described by De Charleroy *et al.* (1990, p. 83), Moravec and Konecny (1994 pp. 67–68) and Kennedy (2007, pp. 324–329) and are summarized here. The life cycle includes maturation and reproduction within the eel final host, a crustacean intermediate host that is required for

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larval development, and various aquatic organisms that may serve as paratenic (transport) hosts. Eggs are deposited within the eel swimbladder by the female nematode and quickly develop into second stage larvae that may remain within the egg case. The second stage larvae are expelled through the pneumatic duct (a connection between the swimbladder and alimentary canal) and hatch quickly within the digestive tract. After passing through the digestive tract, second stage larvae attach themselves to the substrate within 2 or 3 days. Second stage larvae may survive and remain infective for 8 months at 7°C (45°F) and 5 months at 24°C (75°F). To moult and become infective third stage larvae, second stage larvae must be eaten by a crustacean intermediate host, usually a copepod but sometimes an ostracod (Moravec and Konecny, 1994, pp. 67–68). If the crustacean host is then eaten by a paratenic host—these include various small fishes, snails and aquatic insect larvae—then the third stage larvae will survive for a period of time and remain infective, but it will not mature. Eels that eat either the intermediate host or the paratenic host become infected by the third stage larvae, which migrate through the intestinal wall to the swim bladder. The larval nematodes parasitize the blood supply of the swimbladder wall, moult several more times, mature, and ultimately reproduce. Under laboratory conditions at 20°C (68°F), the life cycle can be completed in as little as 2 months.

Cold water temperature limits the distribution of *Anguillicoloides crassus*, as determined by laboratory experiments and the distribution of infected eels in the wild. Eggs of *A. crassus* do not hatch below 10°C (50°F) (Szekely *et al.* 2009, p. 207). Parasite prevalence (percent of eels infected by *A. crassus* parasites) and intensity (number of *A. crassus* parasites per infected eel) were reduced in cold winter temperatures less than 4°C (39.2°F) (Thomas and Ollevier 1993, p. 211; Knopf *et al.*1998, p. 148; Fenske *et al.* 2010, p. 1704). When infected eels were held for 4 months at 4°C (39.2°F), adult *A. crassus* in the swim bladder exhibited starvation, reproductive failure and high mortality (Knopf *et al.*1998, p. 148). The parasite is not found in the cold waters of Newfoundland (Aieta and Oliveira 2009, p. 234). Infected eels in Sweden are primarily found in the warm discharge of a nuclear power plant on the south coast (Hoglund and Andersson 1993, p. 115).

Mean parasite intensity is significantly lower in brackish water compared to fresh water (Morrison and Secor 2003, p. 1492). Salinity and parasite prevalence varied significantly among Chesapeake Bay eels—parasite prevalence was 72 percent and 42 percent in two freshwater (less than 10 ppt) upper bay locations, compared to 18 to 41 percent at four brackish water (less than 26 ppt) lower bay locations (Fenske *et al.* 2010, p. 1706). Kirk *et al.* (2000, p. 215) found that third stage larvae were infective to intermediate and paratenic hosts for up to 80 days in fresh water, but only 8 days in sea water. Higher salinity also reduced hatching success and second stage larval survival (Kirk *et al.* 2000, p.214). A threshold salinity value of about 15 ppt interferes with the development of *Anguillicoloides crassus* and impairs life cycle completion (Lefebvre and Crivelli 2012, p. 199). In infected eels, *A. crassus* depends on the host's osmotic and ionic regulation of the environment in

the swimbladder (Kirk *et al.* 2000, p.217). Despite the protection afforded by the host's internal environment, up to 10 percent of the parasites died in infected eels exposed to sea water for 12 weeks (Kirk *et al.* 2000, p.217) demonstrating that the internal environment of the swimbladder does not fully protect the parasite from seawater, and some likely will die during silver eel migration.

The spread of *Anguillicoloides crassus* in the Americas and Europe may be facilitated by the number and variety of paratenic and intermediate hosts—currently at least 20 species of small fishes as well as snails, amphibians, and insects are known to harbor the parasite larvae (Kennedy 2007, p. 324). In contrast, no paratenic hosts have been identified in the endemic Pacific region (Szekely *et al.* 2009, p. 207). Machut and Limburg (2008, p. 42) found lower parasite prevalence and reduced parasite intensity upstream of physical barriers and concluded that the upstream movement of infected eels and the various parasite hosts appears to be inhibited by dams and natural waterfalls. Installing eel fishways at dams and trapping/transporting eels to upstream waters results in parasite transmission to upstream waters. With regard to parasite transmission *among* watersheds, vectors include the movement of infected eels between adjacent estuaries, transporting infected eels to new watersheds, or ballast water transfers that carry infected eels or paratenic hosts (Rockwell *et al.* 2009, p. 484). Ballast water discharges may also explain the higher rates of infection in rivers with large ports (Aieta and Oliveira 2009, p. 234).

The large scale dispersal of *Anguillicoloides crassus* has been via anthropogenic means, primarily the transport of infected eels over long distances. The importation of infected eels from Taiwan in about 1980 introduced *A. crassus* into eel aquaculture farms in northern Europe (Kennedy and Fitch 1990, p. 118; Køie 1991, <u>in</u> Barse and Secor 1999; Wielgoss *et al.* 2008, pp. 3490–3491). The parasite then spread throughout Europe from this initial introduction. Kennedy and Fitch (1990, p. 129) documented that the parasite was introduced to multiple locations in Britain prior to 1987 due to the importation and subsequent transport of infected live eels for the restaurant trade. Nearly three decades after the initial European introduction, Wielgoss *et al.* (2008, pp. 3490–3491) analyzed genetic samples of *A. crassus* from sources throughout Europe and demonstrated that the spread of *A. crassus* was due to the single initial introduction of aquaculture eels from Taiwan, and that further expansion resulted primarily from the translocation of eels within Europe. For example, infected eels were introduced into Great Britain by 1987 but did not reach Ireland until 1998 when infected eels from England were stocked in Ireland (Evans and Matthews 1999, p. 667).

In North America, *Anguillicoloides crassus* was originally found in 1995 at two separate locations, an American eel aquaculture operation in Texas and from a single wild eel captured in Winyah Bay, South Carolina (Fries *et al.* 1996, pp. 795–796). The spread of *A. crassus* in North America generally has been outward from the original occurrence in South Carolina (Moser *et al.* 2001, p. 851). Collections in 1998 and 1999 documented a mean

parasite prevalence rate (percent infected) of 52 percent in the Carolinas where the parasite was originally found, but only 10 to 29 percent in Chesapeake Bay and less than 12 percent in the Hudson River (Moser *et al.* 2001, p. 848). A more recent study by Hein *et al.* (2014, p. 204) found the same pattern of reduced parasite prevalence with latitude, although prevalence had increased at all three sites—South Carolina (58 percent), Chesapeake Bay (41 percent), and New York (39 percent). In general, *A. crassus* infection prevalence has increased after initial introduction to a watershed (Morrison and Secor 2003, p. 1487). Over time, the parasite has also spread upstream within watersheds (Morrison and Secor 2003, p. 1494), as far as 285 km (177 mi) in the case of the Potomac River watershed (Zimmerman and Welsh 2012, p. 135).

Surveys conducted since the early 2000's have examined eels from rivers in New England from the Pawcatuck River in Rhode Island to the East Machias River in Maine. The parasite is widely distributed in these waters with 7 to 76 percent of the eel containing some life stage of the parasite (Aieta and Oliveira 2009, pp. 232–233). Prevalence may be lower in smaller eels—Roanoke River eels from 101 to 200 mm (4 to 8 in) had a mean prevalence of 20 percent while eels from 145 to 237 mm (6 to 9 in) had a mean prevalence of 27 percent (American Eel Working Group 2010, p. 1). In Canada, sampling through various programs in 2002 to 2005 found no *Anguillicoloides crassus* in Canadian waters (COSEWIC 2012, p. 74). However, in 2007, the parasite was found in Cape Breton, Nova Scotia, far from known occurrences in the United States and was hypothesized to originate from ballast water transferred in the Strait of Canso or Bras d'Or Lake (Rockwell *et al.* 2009, p. 484). In 2006 through 2010, eels were purchased from commercial fishers in Nova Scotia, marked, and stocked in the upper Saint Lawrence River/Lake Ontario (SLR/LO) watershed as an enhancement strategy. Marked eels that were infected with *A. crassus* were subsequently caught in the upper SLR/LO in 2010 through 2014, although parasite prevalence has remained low at about 1 percent (Ontario Ministry of Natural Resources (OMNR) 2014, p. 115; Pratt et al. 2015).

Anguillicoloides crassus infections cause physiological damage to the swimbladder, with the extent of damage proportional to the number of parasites present and the duration of parasite infestation (Szekely *et al.* 2009, p. 208–209). However, the buoyancy regulation function of the swimbladder is not much of a concern for yellow eels since they primarily use benthic habitats. Rather, buoyancy regulation is needed by silver eels during their spawning migration, as indicated by the diel vertical migrations to depths that sometimes exceeded 600 m (3281 ft) (Aarestrup *et al.* 2009, p. 1660; Westerberg 2014, pp. 91–94). Laboratory studies in the European eel have shown that light (approximately 5 nematodes per eel) and moderate infections can reduce eels' swim capacity, perhaps by as much as 10 percent (Sprengel and Luchtenberg 1991 <u>in</u> Moser *et al.* 2001, p. 851). Würtz *et al.* (1996 <u>in</u> Kirk 2003, p. 390) demonstrated that adult parasite intensities of greater than 10 adult parasites per eel can reduce the proportion of oxygen in the swimbladder of adult eels by

approximately 60 percent when compared to uninfected eels. Simulated swimming experiments in European eel indicate that heavily parasitized eels (20 or more parasites) experience decreased swimming efficiency and possibly reduced buoyancy (Szekely *et al*. 2009, p. 217). The authors estimated that heavily infected European eels would require about 20 percent more time to migrate to the Sargasso Sea.

Parasites cause the swimbladder to shrink, resulting in higher costs of transport (van den Thillart *et al*. 2005, p. 105). The adult parasite typically lives for several months and may persist during outmigration (van den Thillart *et al*. 2005, pp. 7, 233; USFWS 2006, p. 2). Experimental results have shown that the parasites exhibit starvation, reproductive failure, and high mortality at temperatures below 4°C (39°F) (Knopf *et al*.1998, p. 148), which were typical at the daylight migration depths documented in the first few months of European eel marine migration (Westerberg 2014, p. 94). With regard to the physiological condition of migrating silver eels, Sjoberg *et al*. (2009, p. 2158) found no significant differences in body fat content, condition indices or estimated migration speeds between infected and uninfected migrating European silver eels.

According to Knopf and Mahnke (2004, p. 494), Japanese eel are not affected by *Anguillicoloides crassus* to the degree that a non-adapted host, such as the European eel (and presumably American eel). The authors noted that Japanese eel produce antibodies as a defense mechanism against *A. crassus*, likely due to co-evolution with the parasite, which results in a balanced host–parasite system without significant harm to the host. Studies suggest that there also may be a level of immunity that develops in both American and European eel, and parasite infection may be reduced by antibody response (Kirk 2003, pp. 390, 391; Szekely *et al*. 2009, p. 208). Ashworth *et al*.(1996, p. 303) and Ashworth and Kennedy (1999, p. 289) identified several density dependent mechanisms that reduce infection prevalence and intensity—infected copepods survived only 12 days versus about 30 days for uninfected copepods. In addition, they found that heavily infected copepods may die before the larvae reach the infective third stage, and the presence of adult males and females in the swim-bladder, particularly gravid females, appears to inhibit larvae from entering the swimbladder and maturing (Ashworth and Kennedy 1999, p. 289).

Anguillicoloides crassus infection does not normally cause outward signs of disease among American eel (Barse and Secor 1999, p. 7). Despite the pathological changes and degeneration of the swimbladder caused by *A. crassus* infection, no outer symptoms are observable on infected eels (Szekely *et al*. 2011, pp. 212–213). Studies find no lack of appetite in infected European eels or difference in condition factor, even among heavily infected eels (Køie 1991 in Szekely *et al*. 2011, p. 212; Koops and Hartmann 1989 in Szekely *et al*. 2011, p. 212). The length/weight relationship does not differ between infected and uninfected European eels and there is no significant difference in weight between infected and uninfected eels (Barus and Prokeš 1996 in Szekely *et al*. 2011, p. 212). Similar results were found among Chesapeake Bay American eel where parasitism

was unrelated to growth or mortality and American eels with swim bladder damage did not differ in age or growth rate relative to individuals that lacked swim bladder damage (Fenske *et al*. 2010, p. 1708).

The prevalence and intensity of *Anguillicoloides crassus* infection in rivers and estuaries appears to be mediated by certain environmental conditions. As described earlier, there is a lower prevalence of *A. crassus* in higher salinity waters (Barse *et al*. 2001, p. 1367; Fenske 2010, p. 1706), with a threshold salinity value of about 15 ppt that impairs *A. crassus* development and life cycle completion (Lefebvre and Crivelli 2012, p. 199). Also, parasite survival is lower at temperatures below 4°C (39°F) (Thomas and Ollevier 1993, p. 211; Knopf *et al*.1998, p. 148; Fenske *et al*. 2010, p. 1704), which may account for observed lower parasite intensity during fall and winter (Fenske 2010, p. 1708) and the absence of the parasite in northern waters (Aieta and Oliveira 2009, p. 234).

6.2.2   PSEUDODACTYLOGYRUS BINI AND P. ANGUILLAE

Pseudodactylogyrus bini and *P. anguillae* are closely related exotic species of parasitic flatworms that are sometimes found on the gills of American and European eels. The biology and life history of these non-native parasites are described by Buchman (1987, pp. 52–55) and Kennedy (2007, p. 321) and are summarized here. The adult flatworms shed eggs into the water column where they hatch to produce a short lived larval stage. The larvae must find a yellow eel and attach to the gill tissue to develop into an adult. The optimal conditions for *P. bini* are warm fresh waters, whereas *P. anguillae* can tolerate brackish water and low temperature. *Pseudodactylogyrus bini* overwinters as eggs, whereas *P. anguillae* may overwinter on gills and is generally the more common of the two species. The abundance of both species is greatly reduced in winter. Optimum water temperature for reproduction is 20 to 25°C (68 to 77°F) which results in a generation time of about 11 days.

The two *Pseudodactylogyrus* species are widespread in Europe where they were first reported from an eel aquaculture facility in western Russia in 1977 that imported infected Japanese eels (Buchmann 1987, p. 52). The subsequent transfer of infected cultured eels rapidly spread the parasites to European eel stocks throughout eastern Europe. The parasites are common in North America where they were likely introduced earlier than *Anguillicoloides crassus* (Kennedy 2007, pp. 321–322). Hayward *et al*. (2001, pp. 58–59) concluded that *P. bini* and *P. anguillae* were introduced into North America by the early 1990s and possibly as early as 1978 in shipments of live foreign eels for aquaculture purposes. Ballast water transfers may also account for introductions of *P. anguillae*, but are unlikely to account for the introduction of *P. bini* since it has very little salinity tolerance (Hayward *et al*. 2001, p. 58).

The two *Pseudodactylogyrus* species appear to cause few, if any, problems to wild eels (Kennedy 2007, p. 322). Although the parasite may cause gill tissue damage and impair

respiration among infected wild American eels, it does not appear to cause direct mortality or to have any effect on eel migration (Kennedy 2007, p. 322). Pathogenic effects have been noted only in aquaculture conditions where the high density of *Anguilla* sp. found in fish farms allows *P. bini* infections to reach very high intensity and causes cultured eels to cease feeding and sometimes die under conditions of high temperature, low oxygen, and high fish density (Kennedy 2007, p. 322).

6.2.3 SUMMARY

The exotic parasite *Anguillicoloides crassus*, has become well established in continental waters of the western North Atlantic. The distribution of the parasite continues to expand with new watersheds becoming infected. In previously infected watersheds, parasitized eels, and possibly paratenic hosts, are expanding the range upstream. In addition, there is some evidence that mean *A. crassus* infection rates have increased, although the parasite does not typically kill infected eels. These trends mirror the progression of the *A. crassus* infestation about a decade earlier in Europe.

With regard to sub-lethal effects, van den Thillart *et al.* (2005, pp. 233, 236) hypothesized that a swimbladder that has been damaged by *Anguillicoloides crassus* interferes with buoyancy control, which may decrease swimming efficiency and impair buoyancy compensation at preferred daytime migration depths in the open ocean. The authors hypothesize that heavily infected European eels may not complete the up to 5,500 km (3,400 mi) migration from Europe to the spawning grounds in the Sargasso Sea. There is a significant level of uncertainty about the impact of *A. crassus* on the American eel during outmigration and spawning, which cannot easily be studied under natural conditions. In summary, despite increasing mean infection rates over time, there is no direct evidence to support a conclusion that the parasite does cause significant eel mortality. Nor is there direct evidence to support or refute the hypotheses that *A. crassus* impairs the silvering process, prevents American eels from completing their spawning migration to the Sargasso Sea, or impairs spawning.

The introduction and spread of two non-native *Pseudodactylogyrus* species has followed a similar trajectory over a similar period of time. These species were introduced as a result of the importation of infected aquaculture eels and then spread to wild American eels. These parasites can result in serious epizootics in aquaculture settings, but do not appear to cause problems in the wild.

6.3 HABITAT LOSS IN ESTUARIES, LAKES, AND RIVERS

The following sections describe the stressors posed by the loss of some American eel habitats, and impeded access to other habitats. The first three sections address habitat loss

in estuaries, lakes and rivers. These are followed by sections describing how barriers affect local eel population demographics and a summary section.

6.3.1 ESTUARY HABITATS

Estuarine habitats used by American eels have been previously lost due to filling and conversion to upland, eutrophication, and contaminants—current nationwide annual rates of estuarine habitat loss are estimated at 0.9 percent averaging 2,240 ha (5,540 ac) annually (Dahl 2006, p. 16). According to the 2006 Status and Trends of Wetlands in the Conterminous United States, coastal wetlands are still being lost, but at a slower rate than in prior reports. Human-caused loss of deep salt water in coastal Louisiana accounts for much of the recent coastal wetland loss (Dahl 2006, p. 16). Hurricanes can also transform coastal habitats, but the effects of this transformation of habitats on the American eel have not been studied. For example, the U.S. Geological Survey (USGS 2006, pp. 1–2) estimated that 25,900 ha (64,000 ac) of marsh in southeastern Louisiana were lost to open water as a result of hurricanes Katrina and Rita.

From the 1950s to 1970s, substantial amounts of estuarine wetlands were dredged and filled extensively for residential and commercial development and for navigation (Hefner 1986 in Dahl 2006, p. 48). Since the mid-1970s, however, many of the nation's shoreline habitats have been protected either by state or Federal regulations or public ownership (Dahl 2006, p. 48).

Channel dredging and overboard spoil disposal associated with wetland development are common throughout the Atlantic coast. Dredging changes estuary depth and salinity and may alter the distribution of American eels. Additionally, dredging associated with whelk and other fisheries may damage benthic habitats used by American eel (ASMFC 2000, p. 42). However, reviews have not identified any studies or reports that quantify the impacts of dredging and overboard spoil disposal upon American eel habitat.

The two largest estuaries in North America are both on the eastern seaboard and support American eels: the Chesapeake Bay and the Albemarle-Pamlico Sound. Chesapeake Bay and its tidal tributaries have over 17,700 km (11,000 mi) of shoreline, more than the entire west coast of the United States. Albemarle-Pamlico Sound in North Carolina is the second largest estuary in the United States with roughly 600,000 ha (1.5 million ac) of brackish estuarine waters (EPA 2006, pp. 3–4).

Despite the above mentioned habitat loss, large amounts of estuarine habitat remain from Maine to Texas. This important habitat remains available to American eels, and commercial harvest data, fisheries surveys, and research data document that the current estuarine distribution of yellow eels reflects the historical distribution in estuary habitats (Helfman *et al.* 1984, p. 135; Morrison *et al.* 2003, pp. 91–92, see section 4.0).

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6.3.2 Lake, Reservoir and Wetland Habitats

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, p. 481; Casselman 2003, p. 255). Studies by Oliveira *et al*. (2001, pp. 947–948) showed that the greater the amount of lake habitat within a watershed, the more the sex ratio favors females. There are numerous lakes within the distribution of the American eel, many of which have likely been effected by water quality issues or exotic species invasions. American eels have been denied access to some historical lake habitats due to barriers (see section 6.3.4), such as prior dam construction, and the operation of these dams may inhibit eel passage (e.g., by eliminating leakage at spillways). We are not aware of new dam construction in the species' range. Below we present information in the context of the American eel in Lake Ontario and Lake Champlain, both within the Saint Lawrence River drainage.

Access to Lake Ontario and other Great Lakes by American eel was restricted to passage via lock after the building of hydroelectric facilities on the St. Lawrence River. However, the building of canals also opened new avenues and even provided passage past the natural barrier of Niagara Falls and access to the entire Great Lakes watershed. Eels migrating into the Great Lakes and Finger Lakes basin in New York historically had one route through the Gulf of St. Lawrence and up the St. Lawrence River to Lake Ontario. Once in Lake Ontario, the eels could access a large number of tributaries in the United States or Canada, but were blocked from Lake Erie and the upper Great Lakes by the natural barrier at Niagara Falls. With the opening of the Erie Canal in 1825, and later, the New York State Barge Canal in 1928, a second route up the Hudson River and through the canal system was created, allowing eels another access route to Lake Ontario, the Finger Lakes region of New York, and ultimately the entire Great Lakes watershed (Patch 2006, p. 2). This upstream passage route is still available to American eels, although the frequency of lock operations has likely decreased.

There are two large hydroelectric dams on the St. Lawrence River: Beauharnois and Moses-Saunders built in 1930 and 1958, respectively. Neither power project was built with any provisions for fish passage, although both dams include navigation lock systems that are part of the St. Lawrence Seaway. Eel fishways were installed at Moses–Saunders Dam in 1974 and 2006 and at Beauharnois Dam in 2002 and 2003, following testing of prototype systems (McGrath *et al*. 2003b, p. 162). Prior to the installation of these fishways, upstream eel passage was possible only through the system of locks on the St. Lawrence Seaway. Juvenile eel abundance at Moses-Saunders increased following construction of the Beauharnois fishway (figure 21). Downstream passage at both dams is primarily through the powerhouse turbines, although the locks and infrequent spillage are also available as intermittent downstream passage routes.

Lake Champlain, which is tributary to the St. Lawrence River, also produces predominately female eels. Eel declines in Lake Champlain were noted in the fishery in the Richelieu River (Verdon *et al*. 2003, p. 126). The decline has been mainly related to the rebuilding of two old cribwork dams on the Richelieu River in the 1960s (Verdon *et al*. 2003, p. 136) that impeded access to Lake Champlain by young, up-migrating eels. In 1997, a ladder was retrofitted on the Chambly Dam to enhance eel recruitment, and in 2001, the Saint–Ours dam, downstream, was retrofitted with a similar eel ladder (Verdon *et al*. 2003, pp. 136–137). In 1997, the total eel population at the foot of the Chambly Dam was estimated at 19,650 individuals, and the minimum ladder efficiency was estimated at approximately 57 to 68 percent. Access to Lake Champlain, having been reestablished, now allows American eel access to 120,000 ha (49,000 ac) of habitat (Verreault *et al*. 2004, p. 5).

6.3.3   RIVER AND STREAM HABITATS

Loss of access to fluvial habitats (flowing water habitat found in rivers and streams) has negatively affected American eel (ASMFC 2000, pp. 35–39) by decreasing the distribution and abundance of American eel. However, most of the loss of access to riverine habitat occurred prior to 1960 (i.e., very few new dams have been built in the American eel range since 1960) and we have no information on ongoing or future dam construction that may further restrict the species' range. In addition, upstream passage facilities built specifically for American eel are becoming more common, which is improving access to river and stream habitats.

Lary *et al*. (1997, pp. 1–3) conducted a preliminary analysis of stream habitat availability for diadromous fish in Atlantic coast watersheds. They reported that 15,115 dams from Maine to Florida have the potential to hinder or prevent upstream and downstream movement of fish such as eels, resulting in a potential restriction or loss of access to a maximum of 84 percent of the stream habitat within the Atlantic coastal historical range. However, 65 percent (9,728) of the dams from Maine to Florida are less than 7.6 m (25 ft) in height and eels are known to be present above some of these dams. For example, eels were present upstream of nine dams with no eel passage facilities on the Penobscot River, Maine in numbers that supported a commercial silver eel fishery (ASA 2009, p. 1–2). Regional analysis of two watersheds in the South Atlantic area noted that eels remained present upstream of many barriers, until those barriers reached 15 m (50 ft) in height (Cantrell 2006, pp. 4–5). Analysis of dam height and American eel distribution in Puerto Rico indicated that half of the dams that were 1.9 m (6.2 feet) or higher blocked American eel (Cooney and Kwak 2013, p. 182). Of the 15,115 dams noted above, only 7 percent are for hydroelectric power and could result in downstream passage mortality due to turbine passage (Lary *et al*. 1997, p. 3).

Most barriers are thought to have been in place before the 1960s. Castonguay *et al*. (1994, p. 484) considered major habitat modifications to be a potential cause for the extreme

decline of American eels in the Lake Ontario and Gulf of St. Lawrence ecosystems. Anthropogenic (human-caused) habitat modifications in the Lake Ontario and St. Lawrence River ecosystem occurred mostly before the 1960s, whereas the eel upstream migration decline noted at the Moses–Saunders Dam started only in the early to mid-1980s. Castonguay *et al*. (1994, pp. 484, 486) proposed that the lack of temporal correspondence between permanent habitat modifications—the two St. Lawrence River dams were built in 1930 and 1958—and the start of the regional decline evident in the SLR/LO argues against the role of habitat loss in the decline, as the decline should have been evident earlier than the 1980s, although panmixia should have offset the effect of region-specific loss of eel production.

Stream flow velocities can affect the upstream migration of elvers (Jessop 2000, pp. 515, 520) due to their smaller size and weaker swimming ability. However, reduced velocities due to seasonal or operational changes of managed flows have likely provided periods when velocities are passable for migration. The elver's ability to find paths around these velocity barriers has also been documented (elvers have strong climbing abilities and small elvers can negotiate wetted vertical surfaces) (Jessop 2000, p. 520; Craig 2006, pp. 2–4).

6.3.4   BARRIERS AND YELLOW EEL DISTRIBUTION

The effect of dams on upstream eel migration appears to be site specific. Dams may be complete barriers to American eel, they may be partial barriers that obstruct certain sizes of eels, they may only obstruct eels during specific flow conditions, or they may be passable under a wide range of flow conditions and have very little impact on upstream eel abundance. For example, a steep vertical barrier has a different effect on small eels (i.e., YOY), which can climb wetted surfaces, particularly at leakage locations or at the dam abutments, as opposed to yellow eels that are likely to be too heavy to rely upon surface tension to climb vertical wetted surfaces. Eels can also ascend dams via cracks or other interstices in the dam structure. Thus, the specific configuration of a barrier, and the location within the watershed, will dictate its effect. The degree to which a barrier obstructs passage is generally related to the type of barrier (i.e., hydroelectric dam, weir, defunct mill dam, or a dam for recreation, water supply, or navigation), as well as how the barrier is operated, its general condition (those in poor repair are more likely to have rough areas or spillage, both better for eel), whether it was equipped with eel or other fish passage, and other site-specific conditions (Goodwin and Angermeier 2003, pp. 532–533; USFWS 2005, pp. 16–19). Beyond these general characteristics, Lary *et al*. (1997, p. 3) suggested that site-specific assessments are needed to analyze the effects of barriers upon American eel. The authors suggested that 84 percent loss of freshwater habitat for the American eel was a maximum estimate that might be used as a starting point for future scientific studies.

Upstream passage effects are mitigated by the construction of upstream passage facilities dedicated to eels (sometimes called "eelways"). When eel fishways are constructed at

hydroelectric projects, it is typically pursuant to a Service prescription under authority of Section 18 of the Federal Power Act (16 U.S.C. § 791a, et seq.). One of the earliest eel fishways was the Moses-Saunders fishway described earlier, but many more have been built, including eel fishways at non-power dams. These upstream eel fishways generally are narrow inclined ramps with textured substrate, a small flow of transport water, and various attraction flow configurations. Many have been equipped with traps to enumerate upstream migrants and evaluate the effectiveness of facilities. The fishways typically pass several thousand young yellow eels in a season lasting several months, although the Roanoke Rapids Project fishway passed 820,000 eels in 2013, the fourth year of operation (Dominion Electric Environmental Services 2014, p. 3). Most eel fishway evaluations have been unable to assess attraction to the facility, but properly designed, operated and maintained eel fishways can pass close to 100 percent of the eels that enter the fishway (G. Wippelhauser, Maine Dept. Marine Resources, personal communication, Sept 2014). A complete inventory of eel fishways was not available for this report, but partial responses indicate that many eel fishways have been built along the eastern seaboard. Monitoring results indicate that some of these fishways provide safe, timely and effective eel passage at relatively low cost.

American eel distribution research shows that they are present in most of the watersheds that were historically inhabited by the species, although possibly at much lower abundance. For example, a Connecticut River watershed survey verified the distribution of American eel above barriers (Jacobs *et al*. 2004, pp. 325, 330). American eel were the most ubiquitous species of all fish species sampled in the Connecticut River drainage, present in 97 percent of all sites sampled and common in both the main stem rivers and tributary streams (Jacobs *et al*. 2004, p. 325). Electrofishing surveys of the Penobscot and Kennebec Rivers in Maine found that American eel were sometimes the largest fish biomass, and often the most numerous species, particularly in lower reaches (Yoder *et al*. 2006, pp. 35–94). A study of Hudson River tributaries, found that American eels were the most numerous fish within the tributaries surveyed (Machut 2006, p. 49). In general, these surveys document the natural pattern of decreasing abundance of small and medium size eels with distance from the ocean (Smogor *et al*. 1995, 789).

Rangewide, a quantitative analysis of the effects of barriers was based on the best available information for a large number of barriers in North America and the need for barrier-specific information. An update of the NatureServe (2006, 2013) distribution data (figure 9) includes the American eel freshwater distribution information we received from most states within the species' North American historical range. Our analysis, unchanged from the previous 2007 status review (72 FR 4967), indicates that the American eel remains present over roughly 75 percent of its historical U.S. native freshwater range (Castiglione 2006, pp. 1–5).

We conclude that not all structures (natural or human-made) considered barriers to other fish species are barriers to the eel since elvers can pass many barriers, yellow eels can pass

some barriers, and all life stages can use locks. However, we also conclude that there are dams, other human-made structures, and some natural features that may be complete barriers to all American eel. And many dams may be partial barriers that inhibit eel passage or only allow small eels to pass—collectively, these human made structures may have reduced the abundance of American eels in inland waters located upstream of multiple barriers. The fate of eels that are not able to pass upstream of a barrier is unknown. Some researchers hypothesize that eels may find alternative habitat downstream of the barrier, such as the estuary, that overcrowding below the barrier may increase the likelihood the eels will become male, and that below the dams there is likely increased competition, reduced food availability negatively affecting growth rates, and predation (Helfman *et al.* 1987, pp. 48–52; Krueger and Oliveira 1999, pp. 384–387; USFWS 2005, p. 19; Machut 2006, p. 53). Additional eel fishways are needed to mitigate these stressors and expand the freshwater range of American eel.

6.3.5 EFFECTS TO YELLOW EEL DENSITY AND GROWTH

Fish surveys provide information on American eel distribution in relation to barriers, but few studies address the changes in yellow eel population density in response to barriers. Goodwin and Angermeier (2003, p. 533) found that dams can exacerbate the decline in eel density; however, this is clearly demonstrated at only one in three dams within their study area. Machut (2006, p. 51) found in the Hudson River watershed, where there are almost 800 barriers, that the first barrier encountered dramatically reduces eel densities, but did not necessarily result in local extirpation. Densities were highest below barriers, while age, growth (in length), and the number of females increased above barriers.

Two aspects of the eel's life history add complexity to understanding the true effect that decreased density may have on eel reproductive contribution. Densities decrease naturally with distance from the coast, while relative female fecundity increases with lower density (see section 3). Based on these factors, we conclude that low upstream abundance is a natural phenomenon exacerbated to varying degrees geographically by human-made structures and natural barriers, but that relative reproductive contribution is not lost in direct proportion to the decrease in density. Additionally, we conclude that quantifying the impact of barriers on the American eel requires site specific information on the barrier, typical eel sex ratios of an area, the dynamic between lower abundance and the higher probability that females will be produced, density-dependent growth relationships, and length fecundity relationships. Unfortunately, the information to conduct a comprehensive range-wide analysis is not available. And such analyses are complicated by the fact that eel fishways have been installed in many locations in recent years, and more are likely to be installed in the future. This will allow eels to access headwater habitats, but their contribution to the spawning stock biomass will also require safe, timely, and effective downstream passage.

Freshwater and estuarine habitat located downstream of the lowermost barrier in a river remains available to the American eel. In the United States, from Texas to Maine (not including the Great Lakes), over 590,000 km (367,000 mi) of freshwater habitat remain available to American eels downstream of terminal dams or within rivers that do not have significant barriers (such as the Delaware River). For example, 1,860 km (1,153 mi) of river habitat is available to eels on the Connecticut River downstream of the terminal dam, including both the mainstem and tributaries (Castiglione 2006, p. 1–2).

6.3.6 SUMMARY

In general, the distribution of the American eels has not been significantly reduced by barriers, although their abundance may be significantly reduced. Many small barriers do not preclude upstream migration of small American eels (Cooney and Kwak 2013, p. 182). Some dams are passable since they are equipped with eel fishways, or fishways for anadromous species which also may be used by eels. Dams with locks are known to pass eels (e.g., a series of 29 dams and locks on the upper Mississippi River). However, many large hydroelectric dams and storage dams may be complete barriers to upstream migration and thereby reduce the amount of freshwater habitat that is available to eels.

Estuarine, lake, and river habitats provide growth habitat for the American eel. Our current understanding of eel life history shows that a portion of the American eel population completes its lifecycle without ever entering fresh water. Although some estuary habitat has been lost, and we do not know the full extent of these losses, estuarine habitat does not appear to be a limiting factor for American eel. Access to freshwater habitat is effected by large dams constructed for hydroelectricity, water supply, flood control, navigation, and recreation purposes—these dams are passable to some degree if they are equipped with fishways or locks, but otherwise result in a complete loss of eel habitat. We consider most habitat loss from barriers to be a historical effect and population-level effects likely have been realized. We are not aware of future dam construction that is likely to cause significant effect to the American eel. We conclude that although some dams appear to form a complete barrier to upstream migration, American eels are able to negotiate many barriers to varying degrees. Many passage barriers can be addressed by installing eel fishways.

6.4 MIGRATORY EFFECTS FROM HYDROELECTRIC PROJECTS

Hydroelectric projects effect American eel in several ways. The most serious effect of hydroelectric dams is the mortality created by downstream passage—hydroelectric turbines kill or injure a portion of the downstream migrating silver eels that are impinged on intake racks or screens or if entrained in the intakes, killed or injured by turbine structures. If silver eels are migrating during periods with minimal spillage, then a larger portion are entrained and killed. Dams also present a barrier to upstream migrating eels. The degree of

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upstream migration impairment is generally related to dam height (some small dams are likely passable) as well as the specific dam configuration. If upstream fishways are not designed and built specifically for small upstream migrating eels, then upstream habitats are generally unavailable. If upstream eel passage is provided, then downstream migrating eels may pass through turbines and experience direct or delayed mortality. An egg per recruit model used to evaluate eel passage at hydroelectric dams on the Susquehanna River showed that cumulative downstream turbine passage survival at multiple dams must be at least 33 percent to realize any benefit to providing upstream passage over these dams (Sweka *et al*. 2014, p. 771). In addition to downstream and upstream passage effects upon American eel, dams replace lotic (free-flowing) habitat with a much larger quantity of lentic (non-flowing) habitat.

6.4.1 UPSTREAM PASSAGE

Very few studies have evaluated natural mortality rates during upstream eel migration. The number of elvers recruited to the East River, Chester, Nova Scotia during May through July was estimated using mark-recapture methods to be 960,000 elvers (Jessop 2000, p. 514). The population size at recapture sites about 1.3 km (0.8 mi) upstream from late July to October was 2,894 elvers. Although there uncertainties in this type of mark-recapture experiment (e.g., elvers may have returned to the estuary) these data indicate high juvenile mortality rates, in this case at a rate of 99 percent. This high mortality was attributed to the effects of low pH (4.7 to 5.0), predation by fishes including older eels, and high initial elver density which may lead to competition and starvation. Vøllestad and Jonsson's (1988, in Jessop 2000, p. 523) research indicates that eel mortality in fresh waters is density dependent when elver numbers exceed a certain abundance. According to Jessop (1998 in Jessop 2000, p. 523), oceanic conditions may deliver relatively high quantities of elvers to rivers to the point where elver abundances exceed the available habitat capacity (Jessop 2000, p. 523), although elvers may disperse upstream in larger rivers to habitats with lower eel density.

Natural and artificial barriers in rivers impede upstream eel movement. However, upstream migration is typically *entirely* halted only in the cases of the largest dams and waterfalls (Cairns *et al*. 2014 p. 7). Furthermore, upstream fishways specifically for small eels are relatively cheap and easy to install (Haro 2013, entire). Juvenile eels are more abundant below barriers and grow more rapidly if they are able to reach upstream waters with a lower density of yellow eels (Machut *et al*. 2007, p. 1707; Bowser *et al*. 2013, p. 11). In eastern North America, many rivers have multiple dams and may also have natural barriers between the river mouth and headwaters. In such river basins, eels may still be able to colonize upper reaches, but only in a small fraction of the numbers that would occur in the absence of barriers (Hitt *et al*. 2012, p. 1171). The range map shown in this report should be interpreted as the entire area that eels are known to inhabit, including areas where eels are

present only sporadically, or in very low densities. For example, eels are found in the upper Mississippi River upstream of 29 dams, although at very low abundance (see Section 5.6). Where eel occurrence is rare or intermittent, the probability of detecting eel presence increases with the intensity of the search effort.

Model outputs have stressed the overriding importance of providing passage at an initial dam located near the estuary (Lambert *et al.* 2011, p. 1). Improving passage at upstream dams in the watershed without provision of passage at the initial dam did not significantly improve upstream eel densities. In the Hudson River watershed, where there are almost 800 barriers, the first barrier encountered dramatically reduced eel densities but did not eliminate eels from upstream areas (Machut 2006, p. 51). Setting upstream passage priorities among watersheds poses additional challenges. There are differences in growth, fecundity and size at maturity among watersheds and these differences will have an effect on subsequent egg production associated with spawning escapement. Size at maturity within a watershed was found to correlate with the observed back-calculated growth rate of eel from age 1 to age 10 in the watershed (Sweka *et al.* 2014).

6.4.2 Downstream Passage

The biology and phenology of maturation and downstream migration was described in sections 3.6 and 3.7. With regard to hydroelectric project passage, the timing and seasonality of passage at specific hydroelectric projects varies with latitude and is affected by environmental conditions. Downstream migrating silver eels have an inherent diel periodicity with most passage occurring at night, particularly in the hours following sunset (Welsh *et al.* 2014, p. 97; Durif *et al.* 2011, p. 350; Aarestrup *et al.* 2010, p. 268). Eels may sense the correct migration season through temperature and photoperiod cues, but downstream migration events in rivers are stimulated by precipitation/flood events (Durif *et al.* 2003, pp. 353–354; Gosset *et al.* 2005, p. 1101, Welsh *et al.* 2014 p. 104). American eels migrated downstream during all months of the year except July in a migration and passage study on the Shenandoah and Potomac Rivers in Virginia, with most individuals migrating during fall through spring (Welsh *et al.* 2014, p. 136). In contrast, silver eel migration in Maine occurs from August through October (table 2) with peak passage in response to high river flows. Downstream movement is episodic, with periods of holding (generally less than 1 hour, but may be as long as 10 days) prior to passing each hydroelectric station (Durif *et al.* 2003, p. 354; Carr and Whoriskey 2008, p. 397; Welsh *et al.* 2014, p. 74).

Hydroelectric dams are obstacles that delay migration and cause mortality. Silver eel maturation and migration also may be reversed if they encounter significant obstacles or undue delay. Silver eels that encounter a hydroelectric station either pass immediately, or are delayed and exhibit characteristic searching behaviors including reversing direction, changing depth, swimming laterally, moving back upstream, or a combination of these

behaviors (Jansen *et al.* 2007, pp. 1441–1442; Brown *et al.* 2009, pp. 287–288). The median time to pass five dams on the Shenandoah River in Virginia was 18 days (Welsh *et al.* 2014, p. 74). Despite the presence of fish bypass with a uniform acceleration weir-entrance structure, 89 percent of telemetered eels passed through the turbines at a hydroelectric station on the Connecticut River, Massachusetts (Brown *et al.* 2009, pp. 277, 287).

Some eels become entrained in powerhouse intakes during outmigration and either survive, are injured, or die (Electric Power Research Institute (EPRI) 2001, p. 3–1). The highest rate of mortality occurs in smaller turbines and turbines that rotate faster. Turbine mortality disproportionately affects large fecund female eels, since these eels are often found in headwater habitats that may be located upstream of multiple hydroelectric dams. This may skew sex rations since male eels produced in brackish habitats are not subject to turbine mortality (with the exception of a few tidal barrages). Furthermore, the degree of injury and mortality increases with larger eels (EPRI 2001, p. 3–8), suggesting that mortality rates of large female eels may be disproportionately higher than mortality rates of males. Turbine mortality to eels has also been shown to be affected by dam size, turbine type, and percent of maximum load (i.e., higher efficiency results in lower mortality). Eel mortality is also related to specific operating conditions which include nighttime versus daytime operation (eels tend to outmigrate at night), peak versus off peak power production, proportion of the river flow passed as spillage, and the behavior of the eels (EPRI 2001, pp. 3–4 to 3–10; USFWS 2005, pp. 30–33). Delayed mortality and sublethal effects such as impaired reproduction and increased predation risk are poorly understood in the American eel (USFWS 2005, pp. 34–36). However, increased risk of predation and delayed migration have been observed in anguillid species native to New Zealand (Watene *et al.* 2002, <u>in</u> EPRI 2001, pp. 2–18).

The EPRI report (EPRI 2001, entire) compiles data on eel entrainment and mortality through hydroelectric turbines—turbine entrainment rates were higher than for most fishes due to typical eel length, the timing of migration, and the behavior of silver eels. The mortality rate of entrained eels was highly variable, depending on turbine design, size of eels, and operational conditions. For example, mortality rates of entrained silver eels were estimated at Moses-Saunders and Beauharnois hydropower facilities on the St. Lawrence River. Mortality was 26.5 percent and 25 percent, respectively, after passage through large propeller turbines at the two St. Lawrence River hydroelectric stations, based on recovery of large eels with turbine tags (timed flotation telemetry tags) (Normandeau and Skalski 2000). Normandeau and Skalski (2000, p. 4.6) also reviewed studies employing recovery of naturally migrating silver eels at smaller hydroelectric stations and reported survival of 50 to 94.5 percent, with the highest survival observed at bulb turbines with only three blades. However, higher mortality rates have also been reported. For example, Montên (1985, <u>in</u> McCleave 2001b, p. 593) reviewed literature through the early 1970s on injury and

mortality of European eel during turbine passage—injury rates (including death) were from 40 to100 percent based on 730 mm (29 in) eels passing through Kaplan turbines under various operating conditions. Hadderingh (1998, pp 325–327) and McCleave (2001b, p. 611) describe mortality rates ranging from 5 to 60 percent for American eels passing through turbines during downstream migration.

Cumulative mortality refers to the estimated combined mortality from passing multiple dams during the downstream migration within a watershed, and is thought to cause significant reductions in that watershed's eel reproductive contribution to the population. Verreault and Dumont (2003, p. 247) estimated cumulative mortality rates of 40 percent for Lake Ontario's outmigrating female eels that pass through the Moses-Saunders and Beauharnois hydroelectric facilities on the St. Lawrence River. The cumulative impact of multiple hydroelectric projects within a watershed, as simulated by McCleave (2001b, p. 602), indicates substantial decrease in overall eel reproductive contribution from a watershed, even when survival rates of eel passage were high through each successive turbine or dam project. The simulated cumulative mortality within the watershed was approximately 60 percent (40 percent survival) of overall reproductive contribution when mortality per dam was 20 percent (80 percent survival). However, the author states that his model is meant as a tool to compare results based on different inputs, not a definitive statement about cumulative mortality within the watershed. Based on the data available, we can reasonably assume that where American eels encounter one hydropower facility during outmigration, there is a typical mortality rate in the range of 25 to 50 percent, and when one or more turbines are encountered, the mortality rate increases to 40 to 60 percent for that watershed. This leaves escapement values (the percent of individuals who survive to continue outmigration) of a minimum of 40 percent and a maximum of 75 percent. Even if the mortality rate has been underestimated, there are still eels in freshwater areas that are unaffected by turbine passage, and eels that survive passage under specific conditions such as in spilled water.

The 2007 American eel status review (72 FR 4967) noted that of 33,663 dams that are located in the Atlantic and Gulf states, only 4.5 percent (1,511 dams) are hydropower dams. Of these dams, only 2.06 percent are terminal dams (dams closest to the ocean) (Castiglione 2006, p. 1). Terminal dams with hydroelectric turbines affect American eels in the entire watershed since all migrants must pass these dams as they outmigrate. However, hydroelectric dams farther up in the watershed impact outmigrating eels in proportion to the habitat located upstream. Mapping also showed that the greatest density of hydroelectric facilities appear clustered in the Northeast, the piedmont of the Southeast, and the White/Red/Arkansas river basins (Castiglione 2006, p. 2; Cantrell and Hill 2009, p. 919). Still, we cannot estimate the percent of eels subject to turbines.

The effects from turbines to the American eel, experts have suggested, could result in a decrease in local or regional abundance, as well as a population skewed toward smaller and

younger females and more males, and together these changes in the population could ultimately result in a decline in recruitment (USFWS 2005, p. 34). In analyzing the effects of turbines on the American eel, however, we also took into account that turbines principally affect eels in fresh water, leaving the portion of the population that inhabits estuarine and marine waters largely unaffected (USFWS 2005, p. 3). As a consequence, a decline resulting specifically from turbine mortality may be buffered by the spawning input from eels residing in unaffected freshwater habitats as well as those found in estuarine and marine habitats throughout its wide range.

The importance of turbines as a population stressor can be assessed only in the context of a general understanding of distribution and dispersal patterns of the eel. Specifically, a watershed's specific reproductive contribution rates and size distribution of females needs to be accounted for in determining the impact of turbines on anything larger than a watershed level basis (USFWS 2005, p. 31). Currently there is no such rangewide estimate. In lieu of this rangewide estimate, we can look at whether there has been an effect to the American eel population, and if so, whether it relates to the construction of hydropower facilities. As is discussed in section 5, there does not appear to be a rangewide decline in recruitment of glass eels; therefore, we can draw no connection between turbine mortality and population-level impacts. Additionally, according to Castonguay *et al*. (1994, p. 486), the timing of the 1980s decline of the American eel in the upper SLR/LO does not correlate with the human–caused changes that occurred on the St. Lawrence River prior to 1965.

Downstream passage facilities such as weirs (surface or bottom opening) and flumes have been incorporated at many dams to mitigate the effects of turbine mortality. Durif *et al*. (2003, p. 350) found that eels presented with surface and bottom opening bypass weirs preferred the bottom bypass (94 percent), although the bottom opening weir was larger and may have passed greater flow than the surface bypass. A study of silver eel passage at a refurbished hydroelectric plant on the Magaguadavic River in New Brunswick found only 21 percent of tagged eels used a new surface bypass weir, 11 percent passed safely by other routes and the remaining silver eels entered the turbines soon after encountering this route and died, as evidenced by cessation of movement (Carr and Whoriskey 2008, p. 396–398). A bottom opening weir at the Lockwood Dam on the Kennebec River, Maine was 90 percent effective in passing downstream migrating silver eels (G. Wippelhauser, personal communication). Laboratory tests of angled bar racks and louvers (an angled rack with each bar turned perpendicular to flow) have provided effective guidance to bypass weirs (Amaral *et al*. 2003, p. 367). The authors effectively guided 55 to 73 percent of silver eels with various 45-degree angled bar racks and 88 percent of silver eels at most 15-degree louvers. A study of two species of New Zealand eels found that silver eels up to 1 meter long (39 in) could penetrate turbine intake racks with 30 mm (1.2 inch) spacing (Boubee and Williams 2006, p. 172). In contrast, 30 mm (1.2 in) intake racks were large enough to allow

European silver eels to enter, but the authors reported low rates of turbine entrainment (Gosset *et al.* 2005, p. 1104).

Downstream passage solutions have also included operational measures such as nighttime turbine shut down. In a study of the five hydroelectric dams on the Shenandoah River, Welsh *et al.* (2014, pp 75–77) documented individual dam mortality rates ranging from 14 to 36 percent during hydroelectric generation were reduced to 0 to 6 percent during the turbine shutdown periods. The authors concluded that nighttime shutdowns were an effective method to protect downstream migrants, although the seasonal timing of the shutdowns only encompassed 67 percent of the total downstream passage events in the study. Nighttime shutdowns have been implemented to pass silver eels at four dams on the Presumpscot River, Maine, but were not evaluated for effectiveness. This is a very promising downstream passage measure that theoretically can provide up to100 percent passage protection for silver eels (Richkus and Dixon 2003, p. 377), although it is very costly due to lost nighttime generation revenue. Better ability to monitor silver eel migration, or predict environmental factors that trigger downstream migration of silver eels, could greatly reduce the lost revenue incurred by nighttime shutdowns. On the River Erne in Ireland, 54 tons of downstream migrating silver eels were captured in a conservation fishery that operated from 2009 to 2012 and transported downstream of multiple hydroelectric dams to reduce the losses due to turbine entrainment and mortality (McCarthy *et al.* 2014, pp. 29–30).

6.4.3 SUMMARY

In summary, hydroelectric turbines, particularly multiple turbines within a watershed or turbines on terminal dams which effect the entire silver eel run, can cause substantial silver eel mortality within those watersheds. However, turbines are present on a small portion of the dams in Atlantic and Gulf coast watersheds and are absent from most of the barriers encountered in the Mississippi Watershed. Downstream passage facilities—some have been built specifically for silver eels, but downstream passage facilities built for anadromous species are also used by silver eels—have had variable success. Passage over spillways can be very effective, or may incur some mortality depending on the configuration of the spillway. Nighttime shutdowns appear to be very promising if they match the silver eel migration timing on the river and provide a safe alternative to the turbines. Dam removal provides the most effective upstream and downstream passage (Hitt *et al.* 2012, p. 1178). Bernhardt *et al.* (2005, p. 637) documented $7.5 billion that was spent on U.S. stream restoration projects between 1990 and 2003 and noted that many of these projects have improved American eel passage. American Rivers (2013, entire) documented 593 dam removals in the United States between 1999 and 2012, many of which were within the range of American eel.

Some eels survive turbine passage and may complete their migration, even after multiple turbine passage events (Welsh *et al*. 2014, p. 75). Turbine passage survival rates are extremely variable, varying from 94.5 percent to as low as 0.0 percent. Transporting elvers above multiple dams—a management action considered in many areas—may not be beneficial if cumulative mortality during downstream passage as silver eels exceeds the benefits of increased egg production by producing larger and more fecund females in upstream areas (Sweka *et al*. 2014, p. 764). McCleave (2001b, p. 603) concluded that small increases in population density, or increases in female silver eel length, had greater effects on survival and realized fecundity than similar improvements in turbine survival rate. With respect to the entire population of American eel, there is no evidence of a population-level effect from turbine mortality; rather, turbine passage mortality is responsible for decreases in abundance on a local or regional scale and potentially can be mitigated with dam removal, effective bypass facilities, or properly timed nighttime shutdowns. Currently, turbine mortality is not considered a significant stressor to the American eel at a population level.

6.5 COMMERCIAL HARVESTS

American eel harvest occurs throughout the species' freshwater and estuarine range. Most commercial harvest of American eel occurs in the United States and Canada along the Atlantic, where all continental life stages are harvested (figure 10). In the United States, the largest harvest is yellow eels in the Chesapeake Bay region, with smaller fisheries for silver eels in the Delaware River, glass eels in Maine (and limited in South Carolina), and with additional yellow eel fisheries scattered throughout other coastal states. Regulations restrict harvest so that exploitation of life stages differs geographically. American eel fisheries for all life stages are unevenly distributed within Canada. American eel in Canada were designated as Threatened by COSEWIC in 2012 and the species currently has no status under the Canadian Species at Risk Act (COSEWIC 2012, p. 76). Commercial fisheries in Ontario were eliminated in 2004, while those in Quebec have been significantly reduced (COSEWIC 2012, p. 76–77). Limited commercial fisheries exist in some Caribbean islands and possibly in Mexico, including some glass eel harvests (ASMFC 2006, p. 14).

The American eel fishery has changed over time. Eel landings in the 1970s and 1980s were primarily yellow eels and were significantly higher than either before or since that time (figure 25). This historical period of high landings was due to domestic markets for yellow eels, as well as emerging markets for silver eels in Europe and glass eels in Asia (St. Pierre 1998, p. 1). Asian aquaculture operations primarily produce an eel product known as 'kabayaki,' a grilled eel that is very popular in Japan and is also shipped worldwide (Schweid 2010, p. 147). In 2002, Japan consumed 67 percent of the freshwater eels eaten worldwide, but higher prices for kabayaki reduced this consumption to 27 percent by 2010 (Crook and Nakamura 2013, p. 29). American eel landings have declined in the United

States and Canada since the 1980s, which has changed food preferences (i.e., markets), and caused a decline in the prices paid for eels in these markets. However, global markets for the kabayaki product have remained strong (Schweid 2010, p. 147).
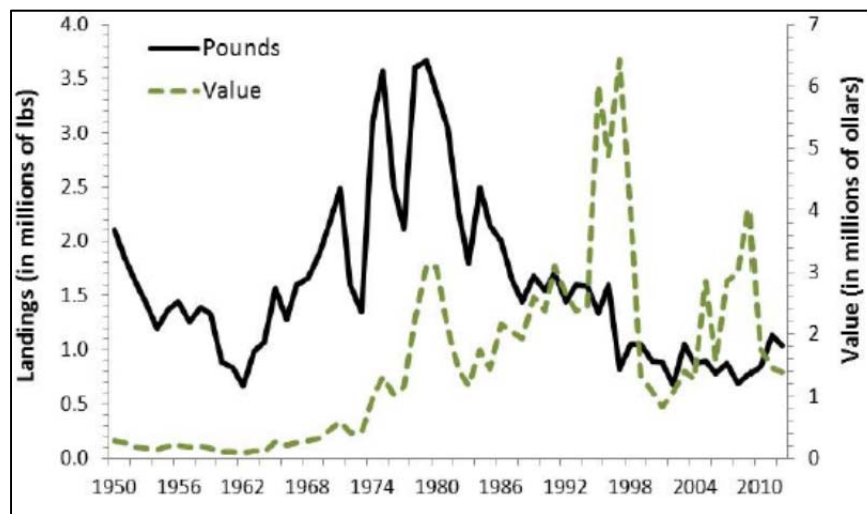

FIGURE 25—Total U.S. commercial landings and value of yellow eels from 1950 to 2010 (ASMFC 2014b, p. 9).

Throughout this five-decade period of fluctuating eel fisheries, the management of American eel has been limited. American eel have not been managed to achieve a specific spawning escapement, as is the current practice in European eel management. An American eel population estimate has never been possible due to the panmictic nature of the species and the distribution over a large geographic area, with the exception of the genetically-based estimate noted above (section 2.3). As a result of enormous data gaps such as spawning escapement goals and population estimates, it has not been possible to manage any of the commercial eel fisheries to meet a specific rate of harvest, sustainable or otherwise. Instead, management efforts have traditionally focused on size limits, gear-type restrictions, and license requirements (i.e., limiting entry) for specific fisheries. A quota of 9,688 lbs has been instituted for Maine's glass eel fishery in 2015, with a coastwide quota of 907,671 pounds for the 2015 yellow eel fishery (ASMFC 2014b, pp. 10, 13).

The current commercial harvest of American eel is driven in large part by the international demand for eel (Pawson *et al*. 2005, entire). In the past, American eel represented a small fraction of the total pounds of eel sold internationally. However, this has increased with the prohibition of European eel exports. China appears to be setting the world price of eels by buying eels on the international market and producing kabayaki size eels in extensive aquaculture facilities (Dekker 2005, p. 2). According to TRAFFIC, a joint program of the World Wildlife Fund and the International Union for the Conservation of Nature, 96 percent

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of global eel production comes from aquaculture, mostly in Taiwan, mainland China, South Korea, and Japan (Crook and Nakamura 2013, p. 25). China supplies about two thirds of the global production of about 280,000 tons of eel. The preferred species for use in aquaculture in Asian countries are Japanese and European eel—American eel are used only to the extent that the two preferred species are not available. The following sections describe commercial exploitation of glass eels, yellow eels and silver eels.

6.5.1 GLASS EEL HARVESTS FOR AQUACULTURE

Fishing for glass eels (sometimes referred to as elvers) began in North America in response to the eel aquaculture industry, located in China, Japan and Taiwan. These Asian aquaculture operations operate on a 1 year cycle and require millions of wild glass eels each year (Moriarty and Dekker 1997 in ASMFC 2006, p. 6). Commercial glass eel fisheries target the spring runs of eels as they enter coastal rivers following their ocean migration from spawning grounds. Glass eel fisheries use dip nets and very small mesh fyke nets placed along stream shorelines to intercept glass eels on the spring migration.

Glass eel fisheries developed in the early 1970s in the States of Florida, North Carolina, South Carolina, Virginia, Massachusetts, and Maine. The glass eel fisheries were unsustainable in Florida, ceased in 1977 in North Carolina, and were prohibited in 1977 by minimum size restrictions of 150 mm (6 in) in Virginia and 100 mm (4 in) in Massachusetts (CBP 1991 in ASMFC 2012, p. 21). In 1992, a 150 mm (6 in) minimum size restriction was imposed by the Potomac River Fisheries Commission, which eliminated glass eel fisheries within its jurisdiction. A small glass eel fishery began in Maine in the late 1970s and continued harvesting small numbers of glass eels through 1993. During the late 1980s or early 1990s, glass eel fisheries were developed or reestablished in Connecticut, Rhode Island, New York, New Jersey, Delaware, and South Carolina, but no historical catch data are available (ASMFC 2012, p. 22). Canadian glass eel fisheries began in 1989 in Nova Scotia and New Brunswick, the only region in Canada where an elver fishery operates (Cairns *et al*. 2008, pp. 3, 41). These fisheries are managed by quota (Chaput et al. 2014a, pp. 69-70). Glass eel fisheries never developed in any Gulf of Mexico states. The FAO statistics include sporadic landings data for Mexico, the Dominican Republic, and Cuba (figure 10) but details, such as the life stages being harvested, are unknown.

The 1999 ASMFC Interstate Fishery Management Plan for American Eel included a 150 mm (6 in) minimum size limit for all states except Maine, South Carolina, and Florida. Gear restrictions in Florida preclude glass eel harvest, and the South Carolina fishery has been limited to 10 licensed individuals. As a result, the Maine fishery lands the majority of the U.S. glass eel harvest. Prior to 1999, participation in the Maine glass eel fishery was unregulated. Beginning in 1999, legislation was enacted to limit the number of licenses, restrict fishing gear, restrict fishing locations, and reduce the length of the season.

As noted earlier, Asian aquaculture is the primary market for glass eel, and this industry prefers Japanese or European glass eel as "seed stock" over American eel glass eel. Thus, the market for American eel is dictated by availability of the other two species—when they are not available in the past, the price for American eel increased dramatically (ASMFC 2012, pp. 4–5, 16, 22). Glass eel prices have been extremely volatile and are currently at record high levels. Anecdotes indicate that maximum American eel glass eel prices in Maine exceeded $2,000 per kg ($900 per lb) in 2011 and $4,800 per kg ($2,200 per lb) in 2012 (Bangor Daily News 2012, p. 1). The Maine Department of Marine Fisheries reported average prices exceeded $4,000 per kg ($1,800 per lb) in 2012 and 2013 (figure 26). The high price in these two years produced the highest Maine elver catches since 1977. In response to ASMFC discussions of quota management for glass eel fisheries, Maine voluntarily implemented a 2014 harvest management plan that included a 35 percent reduction from 2012 levels and in-season monitoring (ASMFC 2014a, p. 3). Although the 2014 quota was 5,329 kg (11,749 lbs), lower prices and cold weather resulted in harvests that fell short of the quota. Assuming there are 2,000 elvers per lb, the Maine elver fishery removed more than 110 million glass eels from Maine rivers from 2011 to 2014, without accounting for illegal harvests.
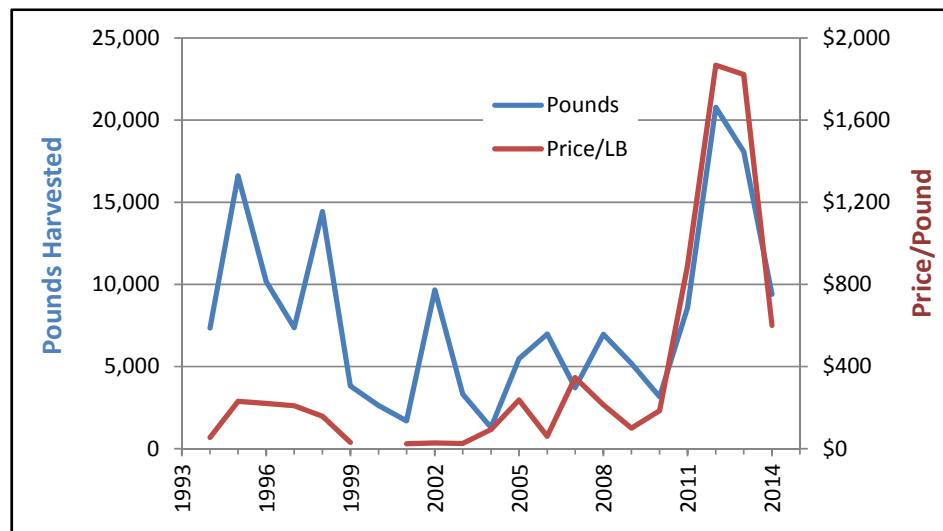
FIGURE 26—Maine glass eel fishery landings and price paid to harvesters from 1994 to 2014. The fishery was managed with limited entry after 1998 and with a quota in 2014 (no price/pound in 2000, preliminary 2014 data) (data from: http://www.maine.gov/dmr/commercialfishing/documents/elver.table.pdf).

Exploitation rates (the percent of mortality associated with harvest) vary with the life stage, fishing gear, and other factors. Glass eels are typically harvested as they enter rivers and estuaries. One study suggests an exploitation rate of 30 to 50 percent of arriving elvers (Jessop 2000, p. 523). If there was no density-dependent change in sex ratio, growth,

survival, or emigration rate in subsequent stages, the reduction in egg production due to the elver fishery would be equivalent to the percent elver exploitation described above. However, such density-dependent effects are believed to occur (ICES 2001, p. 34). In other words, the relatively high exploitation rate for glass eels may not translate to an equivalent proportional reduction in reproduction loss because the glass eels that are not harvested may have a greater potential for survival and, therefore, reproduction. Glass eel fisheries, it has been suggested by Jessop (2000, p. 523), may be biologically justified to a greater degree in Nova Scotian streams with low pH, given the abundance of glass eels entering these streams and the high YOY mortalities that occur during their first summer in fresh water (rather than in more productive streams with higher pH values).

6.5.2 YELLOW EEL FISHERIES

Nineteenth century U.S. harvests of yellow eels are poorly documented, but references such as Bigelow and Schroeder (2002, pp. 94–95) note total harvests of about 2000 tons. In the 20th century, harvests peaked from approximately 1955 to 1985 coincident with increasing market demands from the Chesapeake Bay region crab fisheries and the European food market. By the 1990s, most states experienced declining harvests influenced to an uncertain degree by both the weakening export market and local abundance.

Currently a yellow eel fishery exists to varying degrees in all States and jurisdictions along the Atlantic coast except Pennsylvania and the District of Colombia. The dominant fishing gear for yellow eels in the United States is baited pots, which are used in rivers, lakes, and estuaries. South of Maine, the yellow eel fishery is primarily coastal pot fisheries with a large fishery in Chesapeake Bay—different states have varying regulations, but all states within ASMFC jurisdiction have a 229 mm (9 in) minimum size limit. Different geographic regions on the east coast and Gulf of Mexico have different yellow eel fisheries that reflect influences and stock abundance among the regions. In general, market prices have declined from $3–$4 per lb to $1.25–$1.75 per lb resulting in reduced participation in the pot fisheries. Harvesters report that the low prices are due to eels being grown out in aquaculture facilities (Knights 2003, p. 242), specimens of which, a fish company representative suggests, are better suited to smoking, due to their high fat content and uniform size and shape that is better suited for the current mechanized processing (Feigenbaum 2005, p. 12).

Data from Prince Edward Island, Canada, were used by the authors of the ICES report (2001) to calculate yellow eel exploitation rates. They estimated an approximately 50-percent rate of exploitation in estuary and tidal waters (ICES 2001, p. 41). The authors also estimated how this rate of exploitation would be expressed in loss of reproductive contribution, but based on some significant assumptions, they consider the estimate preliminary. They suggest the effect on reproduction would be a decrease of approximately 90 percent, based on the premise that the largest, and hence most fecund, females are

targeted. However, they also note that the estimated reduction in reproduction for the entire Prince Edward Island area would be less than this value, because there is no eel fishery in non-tidal waters, and there is minimal fishing effort in the central and western portions of the Northumberland Strait, which amount to about one third of the Prince Edward Island coastline (ICES 2001, pp. 34–35).

In characterizing the future effect of harvest, the best available data from literature supports the conclusion that 1970s yellow eel harvest levels are unlikely to occur again due to the changes in eel markets (Pawson *et al*. 2005, p. 6; Dekker 2005, p. 2). Global eel markets have changed due to the interest in eel aquaculture, as opposed to harder-to-process wild-caught eels (Feigenbaum 2005, p. 12), the implementation of harvest regulations (ASMFC 2006, p. 43), and fluctuations in the number of commercial eel fishers (Wippelhauser 2011, p. 2). Although these literature citations are older, we have no newer information to suggest the conditions on which to base our conclusions have changed. This may result in continued pressure to harvest American eel glass eels to supply the eel aquaculture market.

6.5.3   SILVER EEL FISHERIES

Silver eels have been viewed as a high value food fish as a result of their large size and high fat content which produces the highest quality smoked eel product. Various fisheries have employed weirs and nets, in some cases at the same locations for generations. Silver eels become vulnerable to these passive capture methods as they migrate downstream during the fall. Historically, silver eel fisheries have not been nearly as common as yellow eel fisheries in the United States. Traditional silver eel fisheries have operated in Quebec (traps), the Albemarle Sound region of North Carolina (fyke nets), the Delaware River (weirs) and various rivers in Maine (weirs). The largest silver eel fishery was the Quebec fishery employing traps along the St. Lawrence River, although the catch has declined sharply (Robitaille *et al*. 2003; Verreault *et al*. 2003). Under the present ASMFC management plan, very limited silver eel fisheries are allowed only on the Delaware River in New York (ASMFC 2013).

In the St. Lawrence estuary silver eel fishery, mark-recapture experiments estimated exploitation rates of 19 percent in 1996, and 24 percent in 1997 (Caron *et al*. 2003, p. 239). In Canada, there has been a trend towards increasingly restrictive fishing regulations in the last several decades, especially in the Atlantic Provinces, and especially since 2000 (Cairns *et al*. 2005). This could translate, we believe, to a decline seen in Canadian landings data. Changes include shortening of seasons, increases of minimum size, caps on the number of fishing gear that can be deployed, and freezes on development of any new American eel fisheries (COSEWIC 2006, p. 48). There was a buy out of 50 percent of commercial licenses at Lake St. Pierre, the fishery in the Richelieu River was closed in 1998, and the fishery in the upper SLR/LO was closed in 2004 (OMNR 2004, p. 1).

6.5.4 SUMMARY

Commercial harvests of American eel in U.S. waters peaked in the late 1970s and 1980s when large numbers of yellow eels were harvested (figure 25). Harvest trends may reflect changes in eel abundance and it is possible that the large harvests during this period may have constituted overfishing of the stock. However, commercial harvest variability is also affected by emerging markets (e.g., European markets for silver eels in the 1970s and fluctuating markets for glass eels in Asia), consumer demand for eels in these markets, the prices paid to commercial fishers, changes in fishing regulations, and alternative economic opportunities for commercial fishers. It is difficult to determine whether declining eel abundance was a major contributor to declining harvest, versus socioeconomic factors. In characterizing the future effects of eel harvest, the best available data from literature supports the conclusion that 1970s yellow eel harvest levels are unlikely to occur again due to the changes in eel markets (Pawson *et al.* 2005, p. 6; Dekker 2005, p. 2).

Current global markets for freshwater eel are largely driven by the demand for kabayaki, and supplied almost entirely by cultured eels. At the peak of the U.S. eel fishery, less than 2,000 tons of eel were harvested annually (figure 25), with current harvests well under 500 tons (figure 10), less than 0.2 percent of the global annual production of 280,000 tons of eel. However, the harvest of *Anguilla rostrata* glass eels to supply the global aquaculture market remains a concern. As noted above, more than 110 million glass eels (28.4 tons) were harvested from Maine waters in 2011 to 2014. This harvest may have reduced the abundance of young eels in Maine watersheds, and may have an effect on spawning escapement in future years.

6.6 CONTAMINANTS

American eel are long lived and widely distributed among a variety of freshwater and estuarine habitats, potentially exposing them to various pollutants and contaminants over many years. This is particularly true for female eels, and particularly in the northern portion of the range where eels live longer. Contaminants are summarized here in five categories according to the review by Roe (2006, pp. 1–26), as effect of: (1) existing contaminants on the American eel life cycle, including levels of uncertainty and the inability to study various eel life stages; (2) new and emergent contaminants; (3) persistent contaminants, such as genotoxic polycyclic aromatic hydrocarbons (PAHs); (4) nonpersistent contaminants, such as pharmaceutical chemicals and pesticides; and (5) cumulative effects of contaminants.

Contaminants in aquatic ecosystems are regulated under both state and Federal statute. The Clean Water Act of 1972 (CWA), including the major amendments of 1977 and 1987, is the primary Federal law governing water pollution. Under the CWA, the U.S. Environmental Protection Agency (EPA) delegates many of the permitting and regulatory aspects of the law to state governments. In accordance with the Clean Water Act and state statutory

authority, individual states have developed water quality regulations that are comparable to and often more stringent than the Federal regulations. Other Federal regulations that address environmental contaminants include the Water Pollution Control Act and the Federal Insecticide, Fungicide and Rodenticide Act of 1972, Safe Drinking Water Act of 1974, Resource Conservation and Recovery Act of 1976, Clean Water Act and the Soil and Water Resources Conservation Act of 1977, Comprehensive Environmental Response Compensation and Liability Act of 1980, and Oil Pollution Act of 1990. In addition, Canada also has authority to manage water resources and control pollution under two primary acts, the Ontario Water Resources Act and the Environmental Protection Act.

6.6.1   EXISTING CONTAMINANTS

Concentrations of polychlorinated biphenyls (PCBs), PAHs, polychlorinated diphenyldioxins/polychlorinated diphenyl furans (PCDDs/PCDFs), pesticides such as mirex[©] and dichlorodiphenyltrichloroethane (DDT), and metals such as mercury were reported in yellow and silver American eel tissues from eastern U.S. and Canadian waters (Byer *et al*. 2013, entire). However, much uncertainty exists with regard to the population's rangewide contaminant load since environmental contaminant data were only available from a small portion of the species' range; therefore, the contaminant loads within American eel throughout its entire range are unknown.

The contaminant concentrations reported in American eel tissues are within the range of concentrations associated with effects that have been documented in other fish species. These environmental contaminants have been shown to have biochemical, immunological, genotoxic (chemicals toxic to DNA), growth, survival, and reproductive effects on various fish species. We conclude that contaminants therefore have the potential to also effect the American eel (Roe 2006, pp. 5–8). Interestingly, American eels survive with these contaminant loads at concentrations that would be toxic to other fish species. There is, however, a potential for the effects to be fully expressed during critical periods of their life cycle such as metamorphosis, hatching, and larval development (Robinet and Feunteun 2002, pp. 267, 270–272), all of which occur at sea and therefore are currently impossible to research under natural conditions (USFWS 2006, p. 24–27). Because of this species' unique life history, caution was suggested in utilizing surrogate species data in determining effects of contaminants on eels (USFWS 2006, p. 24).

Researchers have not been able to study contaminants on all American eel life stages since it is difficult to complete the American eel life cycle in the laboratory (Penderson 2003 pp. 324, 336–337; Palstra *et al*. 2005, pp. 533–534). In particular, research has not been conducted on the effects of contaminants on eel embryos and leptocephali, or during metamorphosis from the yellow to silver eel stage, or during outmigration and reproduction. Two laboratory studies on the reproductive capacity of European eels by van den Thillart *et al*. (2005, pp. 110, 169) and Palstra *et al*. (2006, pp. 147–148) indicated that preliminary

studies of PCB and dioxin-like contaminant effects to maturation and fertilization showed negative effects on egg quality and embryonic development. However, artificial hormone inducement of maturation in European eels is complicated by high female adult mortality rates and high rates of embryo death after fertilization (Pedersen 2003, pp. 336–337; Knights 2006, pp. 1–2). Therefore, it is difficult to be certain whether the mortality rates are associated with artificial maturation or fertilization techniques or with exposure to contaminants (Knights 2006, p. 2). Byer *et al*. (2013, p. 1445) concluded that overall, the risk to eel recruitment from dioxin-like compounds in American eel using available guidelines is low. Unless or until the issue of embryo death can be attributed exclusively to the presence of contaminants, the data are still inconclusive with regard to the determination of the effects of PCB- and dioxin-like contaminants at a population level in the American eel.

6.6.2   POLYBROMINATED DIPHENYL ETHERS

The effects of new and emergent chemical contaminants in fish are unclear for the American eel. For example, polybrominated diphenyl ethers (PBDEs) are a new group of chemicals that are used as flame retardants in a multitude of consumer products (Agency for Toxic Substances and Disease Registry or ATSDR 2004, pp. 11–12). The PBDEs are similar to PCBs in that they are lipophilic (fat-loving), persistent in the environment, and bioaccumulate in organisms. However, the effects to fish and other aquatic organisms have not been completely defined in the scientific literature. There is evidence that PBDEs cause enzyme activity alterations and delayed embryonic hatching in fish, and they result in behavioral alterations (Largay *et al*. 2006, pp. 1098–1103). Concentrations of PBDEs have been measured in European eels (de Boer 1990, pp. 315–318; Covaci *et al*. 2004, pp. 3851–3855) and in other species (Lebeuf *et al*. 2004, pp. 2973–2976); however, the effects of PBDEs to eels were not discussed. Therefore, extrapolating the effects to the American eel at a population level would be purely speculative.

6.6.3   GENOTOXIC CONTAMINANTS

The effects of genotoxic PAHs on the eel remain uncertain. There is considerable evidence that indicates a causal relationship between exposure to PAHs and genotoxic effects such as tumor frequency, deformities, and other lesions in fish, particularly bottom feeding fish (Black 1983, pp. 328–333; Metcalfe *et al*. 1990, pp. 133–139; Baumann and Harshbarger 1995, pp. 168–170; Baumann *et al*. 1996, pp. 131–149; Johnson *et al*. 1998, pp. 125–134). Couillard *et al*. (1997, pp. 1918–1926) documented the occurrence of precancerous lesions in liver tissues from migrating American eels from the St. Lawrence River. The prevalence of the lesions in the eel liver tissue was reported to be correlated with increasing contamination in eels, and the authors concluded that PAHs may have been the cause (Couillard *et al*. 1997, p. 1924). Research in American eels (Schlezinger and Stegeman

2000, pp. 378–384) and European eels (Doyotte *et al*. 2001, pp 1317–1320; Bonacci *et al*. 2003, pp. 470–472; Mariottini *et al*. 2003, pp. 94–97) has shown that induction of enzyme activity has also been used as a biomarker for exposure to PAHs and similar contaminants. Genotoxic PAHs may be effecting successful outmigration, but effects of lesions and tumors have not been researched under natural conditions or within the laboratory.

6.6.4   NONPERSISTENT CONTAMINANTS

Short term exposure to nonpersistent contaminants during critical American eel life stages may be of concern to the species' viability (USFWS 2006, p. 25), but uncertainty remains. The literature has shown that endocrine disrupting contaminants such as 4-nonylphenol (which is formed during the industrial synthesis of detergents) and pesticides such as atrazine and diazinon cause physiological changes, inhibit growth, and therefore inhibit the survival of wild Atlantic salmon (*Salmo salar*) along the Canadian Atlantic coast (Moore and Waring 1996, p. 758; Fairchild *et al*. 1999, p. 349; Brown and Fairchild 2003, p. 146; Arsenault *et al*. 2004, p. 255; Waring and Moore 2004, p. 93). With regard to American eel, they are exposed to relatively high concentrations of nonpersistent contaminants during their migration through the St. Lawrence River (Pham *et al*. 2000, p. 78). For example, the largest primary physio-chemical municipal sewage treatment plant in North America is located in Montreal, and treated effluent is discharged to the St. Lawrence River (Environment Canada 2006, pp. 1–3; USFWS 2006, p. 25). At this location, there is evidence of endocrine disruption in other aquatic organisms exposed to the effluent from 50 km (31 mi) upstream or downstream of the plant (Aravindakshan *et al*. 2004, pp. 156–164; Gagné *et al*. 2004, pp. 33–43). However, there is no information in the literature on specific locations of these endocrine disrupting nonpersistent contaminants, or on the sensitivity of eels to short-term exposure to them. As a result of this uncertainty, we do not know the potential effect of nonpersistent contaminants to the species' viability.

6.6.5   CUMULATIVE EFFECTS

Finally, contaminants may have cumulative effects due to mixtures of contaminants, dietary deficiencies, or disease. Contaminants can affect the immune system and therefore increase the organism's susceptibility to other stressors such as diseases, parasites, and bacterial and viral infections (Arkoosh *et al*. 1996, pp. 1154–1161; Arkoosh *et al*. 1998, p. 182; Grassman *et al*. 1996, p. 829; Couillard *et al*. 1997, p. 1916; Johnson *et al*. 1998, p. 125; Van Loveren *et al*. 2000, p. 319; Zelikoff *et al*. 2000, p. 325), but the effect on the American eel remains uncertain. The cumulative stress of the complex mixtures of environmental contaminants and other stressors may potentially lead to increased mortality. Contaminants mixed together may interact and have additive effects, as in the case of dioxin (Safe 1990, pp. 71–73; Van den Berg *et al*. 1998, pp. 775–776) or synergistic effects, as in the case of PAHs (Wassenberg and Di Giulio 2004, p. 1662).

6.6.6 SUMMARY

Contaminants may affect early life stages of the American eel, but without specific information, we remain cautious in extrapolation of these preliminary laboratory studies to rangewide population-level effects. A correlation between the contamination of the upper SLR/LO and the timing of the 1980s decline of American eel in the upper SLR/LO is not evident (Castonguay *et al*. 1994, pp. 482–483), and current environmental laws and regulations have significantly decreased the discharge of many persistent environmental contaminants. Given the absence of evidence for population-level effects, such as reduced recruitment of glass eels (which would be an indicator of decreased outmigration, egg, or leptocephali survival), we believe that the available information on contaminants does not indicate a significant stressor to the American eel at a population level.

Because spawning and egg and leptocephali maturation occurs in the open ocean, direct study of the effects of contaminants under natural conditions will continue to be difficult. This emphasizes the need for data collection and analysis designed to differentiate between population fluctuations responding to natural phenomena such as oceanic conditions and those that are human-caused.

6.7 PREDATION

Fish predation upon silver American eels may be significant, based upon studies of silver eels migrating from the St. Lawrence River and estuary. A study using miniature satellite popup tags recorded depth, temperature, and light levels during silver eel migration through the Gulf of St. Lawrence (Béguer-Pon *et al*. 2012, p. 1). Six of eight eels were ingested by warm-gutted predators, as determined by a sudden increase in temperature and changes in swimming depth profiles. Gut temperatures indicate that predation by mammals such as Beluga whale (*Delphinapterus leucas*) or seal was unlikely. Based on the temperature and depth profiles, the investigators concluded that all six silver eels were predated by porbeagle shark (*Lamna nasus*) (Béguer-Pon *et al*. 2012, p. 4). Lower rates of apparent predation were observed when satellite tagged eels were translocated to the open ocean (Wysujack *et al*. 2014, p. 156). Predation may be exacerbated by the hydrodynamic effects of the transmitter tag, which may have affected swimming ability (Burgerhout *et al*. 2014, p. 633), and increased the oxygen consumption (Methling *et al*. 2011, p. 1932), of tagged silver eels. Westerberg (2014, p. 96) reviewed telemetry studies of European silver eels which documented predation by warm-bodied sharks (porbeagle or common thresher (*Alopias vulpinus*)).

Silver eels are sometimes predated by marine mammals. Studies of telemetered European silver eels documented predation by toothed whales (Wahlberg *et al*. 2014, p. 32) and marine mammals (Westerberg 2014, p. 96). Lidgard *et al*. (2014, p. 157) documented a very

low rate of silver American eel encounters with grey seals in the Gulf of St. Lawrence and Scotian Shelf.

A two year acoustic telemetry study monitored the migration of 180 silver eels from fluvial and estuarine portions of the St. Lawrence River to the Cabot Strait in the Gulf of St. Lawrence (Béguer-Pon *et al*. 2014). Overall, 88.9% of tagged eels were detected at fluvial and estuarine detection arrays compared with only 4.0% at the Cabot Strait. The authors could not completely rule out low detection probability at Cabot Strait (e.g., surface migrants may have been as far as 620 m (2000 ft) from bottom mounted detectors). They concluded that a low escapement rate through Cabot Strait may have been the result of a high mortality rate or cessation of migration (Béguer-Pon *et al*. 2014, p. 1590). Westerberg (2014, pp. 100) concluded that, "…it may well be that the predation pressure on migrating (silver) eels is much higher than what is known." Seasonal predation by Atlantic migratory striped bass outside the mouth of Chesapeake Bay upon male silver eels also has been documented (Jim Price, Chesapeake Bay Ecological Foundation, unpublished data; personal communication to R.W. Laney, USFWS, Raleigh, NC). Predation upon glass eels and elvers below dams by fish such as juvenile striped bass has also been observed. Until more data become available on these sources of predation, we cannot draw conclusions that natural marine predation is having a population-level effect on the American eel, nor do we have information to suggest natural levels of predation may be increasing.

7 CONCLUSIONS

Panmixia of American eel has been confirmed (see section 2.2), and thus a single population inhabits the western North Atlantic Ocean and adjacent continental waters. Panmixia is central to evaluating stressors to the American eel since, in order for any stressor to compromise the existence of the population of American eel, it must act upon a large portion of the population at some life history focal point, or the stressor must be present throughout a large part of the species' range. And, the stressor must elicit a response that results in significant mortality, impaired reproduction, or juvenile recruitment failure. Assessing stressors is made more difficult by the lack of a comprehensive American eel life history model—to date, the lack of life history data (e.g., survival between life stages) precludes quantitative stock status assessments and population viability analyses. In particular, the inability to estimate spawner abundance precludes analyses of the number of eel recruits per spawner, an important metric that is needed to assess whether population declines have occurred as a result of stressors in marine versus freshwater habitats. Evaluating the status of the population is very difficult in the absence of these data, but we must use the best available data to draw conclusions.

Harvest data and various elver abundance indices demonstrate that American eel have experienced periods of very low abundance in many locations, particularly during the 1990s and 2000s (see section 5). For example, abundance indicators for the upper SLR/LO stock declined by as much as 99 percent over about two decades (figure 21), and four out of five eel abundance time series from the lower St. Lawrence River and Gulf of St. Lawrence have also declined. Not all eel abundance indices agree—during the same 30-year period that eel stocks declined in the upper St. Lawrence River and Lake Ontario, some eel abundance indices in coastal waters of the Gulf of St. Lawrence tripled (see section 5.7). The only population estimate we are aware of for American eel is the genetically-based estimate of 4.7 to 109 million spawning eel in the Sargasso Sea (see Section 2.3).

There are several life history focal points where stressors may affect the population of American eel, specifically reproduction and migration. Reproduction occurs in a portion of the southwest Sargasso Sea that is defined by specific temperature and salinity criteria (see section 3.1). Similarly, the migration of adults and larvae to and from the Sargasso Sea spawning grounds occurs through areas of the North Atlantic Ocean with specific environmental characteristics, especially currents that may aid eel migration. Section 6.1 reviews various studies that describe correlations between several European and American eel abundance indices and physical oceanographic parameters (i.e., the NAO and Sargasso Sea thermal fronts). The authors of these studies hypothesize how changes in physical habitat may affect eel reproduction and migration, but acknowledge that the studies have not documented the specific causes and effects upon eel life history and biology (Knights 2003, p. 243; Friedland *et al.* 2007, pp. 524–527; Bonhommeau *et al.* 2008, p. 78; Miller *et al.* 2009, p. 244). However, correlation is not causation. In addition, the data sets used in these

studies span only the last few decades when climate indices have shown clear trends, thus superficial correlations might be expected (Knights 2003, p. 238). In summary, although North Atlantic Ocean temperatures may continue to rise as a result of climate change, there remains a great deal of uncertainty regarding changes in physical oceanographic processes and how, or to what extent, they will affect eel reproduction and migration.

The exotic parasite *Anguillicoloides crassus* has become more widespread in and is now present throughout much of the American eel range. The parasite was brought to both Europe and North America as a result of the importation of infected eels and continues to spread. Documentation of the parasite in New Brunswick in 2007 may have been due to ballast water transfer. The range and infection rate of the parasite is naturally limited by low water temperature and high salinity. The parasite does not cause eel mortality, but may impair swimming ability based on swim tunnel tests of infected European eels— heavy parasite infections therefore may reduce an individual's chance of successful spawning. However, similar research with American eel has yet to be undertaken and several factors pertaining to the American eel may indicate less potential effect from *A. crassus*: (1) The mean infection intensities reported for infested waters appear to be moderate; (2) the American eel has a shorter outmigration distance to the Sargasso Sea than European eels; (3) some areas may be free from *A. crassus* infection (Central and South America, the Caribbean Islands, and much of Canada); and (4) areas remain where *A. crassus* is found that are still producing uninfected outmigrating individuals. Caution should be used in extrapolating the European experience with *A. crassus* to American eel, and in using the results of laboratory studies with regard to rangewide implications given the absence of evidence for population level effects, such as reduced recruitment of glass eels (which could be an indicator of decreased outmigration survival). Due to the continued expansion in the United States by *A. crassus* and the long-lived nature of at least a portion of the American eel population, the effect of *A. crassus* on American eel may not yet have been fully realized. Parallels have been drawn to the progression of infection in European eel populations. However, the occurrence of this parasite does not match the timeline for the decline in eel recruitment to European rivers (ICES 2001, p. 6). Furthermore, evidence indicates that morbidity among American eel is less than among European eel.

Several other stressors are present throughout a large part of the freshwater range of American eel. The 2007 American eel status review (72 FR 4967) analyzed habitat loss, barriers to migration, commercial fishery harvests, and contaminants, all of which occur throughout large portions of the species' range. None of these stressors rose to the level that might affect viability of the species. With regard to inaccessible habitat (particularly due to hydroelectric dams), eels are still very widely distributed, estuary and marine habitats are used extensively, and glass eels continue to be recruited to freshwater habitats throughout the range. Although there may be increased predation and mortality at or below dams which block eel migrations, the cumulative effect of such blockages is unquantified.

Commercial fisheries have been significantly reduced in most areas—yellow eel markets have declined and most silver eel fisheries have been closed. The Maine glass eel fishery continues to remove millions of glass eels from Maine rivers; however, this fishery has also been reduced. With regard to contaminants, there are no indications of population-level effects from contaminants—contaminant exposure and effects to American eel are largely unknown.

In summary, the best available scientific and commercial information indicates that despite a population reduction over the past century, American eels are widely distributed throughout a large part of their historical range. Glass eels are recruited to North American rivers in enormous numbers. Elvers are also present in large numbers well inland on some east coast river systems—for example more than 820,000 eels passed through a new fishway at the Roanoke Rapids Dam on the Roanoke River in 2013, the fourth year of operation (Dominion Electric Environmental Services 2014, p. 3). American eels are also plastic in their behavior and adaptability, inhabiting a wide range of freshwater habitats over an exceptionally broad geographic range. Because of the species' panmixia, areas which have experienced depletions may experience a "rescue effect" allowing for continued occupation of available areas without concern for genetic fitness. Trends in abundance over recent decades vary among locations and life stages, showing decreases in some areas, and increases or no trends in other areas. Limited records of glass eel recruitment do not show declines that would signal recent declines in annual reproductive success or the effect of new or increased stressors. Taken as a whole, a clear trend cannot be detected in species-wide abundance during recent decades, and while acknowledging that there have been large declines in abundance from historical times, the species currently appears to be depleted from historical levels but stable.

8 LITERATURE CITED

Additional references can be found in the 2007 American eel Status Review (U.S. Fish and Wildlife Service, 2007).

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