Chapter 7

AMERICAN EEL

(*Anguilla rostrata*)

Section I. American Eel Description of Habitat

American Eel General Habitat Description and Introduction

American eel (*Anguilla rostrata*) are found in fresh, brackish, and coastal waters from the southern tip of Greenland to northeastern South America (Facey and Van den Avyle 1987). Additionally, there may be hybridization, or at least genetic introgression, of American eel into the population of European eel in Iceland. Therefore, the range might possibly be extended to Iceland in the north (Williams et al. 1984; Avise et al. 1990).

American eel are ubiquitous in many habitats (Jacobs et al. 2003), and can contribute up to more than 25% of the total fish biomass in some individual systems (Smith and Sauders 1955; Ogden 1970; J. McCleave, University of Maine, personal communication). In Connecticut rivers and streams, the American eel was found in one case to be four times more abundant than any other species (Jacobs et al. 2003). American eel habitats include the open ocean, estuaries, large coastal tributaries, rivers, small freshwater streams, lakes, and ponds. They utilize habitats from the East Coast of North America and the northern portion of South America, into the inland areas of the Mississippi River and the Great Lake drainages (primarily Lake Ontario), and north into Canadian tributaries. American eel are sometimes found in land locked lakes, particularly in the northeastern United States (Facey and Van den Avyle 1987). The latitudinal range for the American eel has been documented as 5°N to 60°N (Bertin 1956), and their range covers approximately 30,000 km of coastline (Federal Register 2007). American eel are thought to occupy the broadest array of habitats of any fish in the world (Helfman et al. 1987).

American eel are a catadromous species that reproduces in salt water, and after an oceanic larval stage, migrates to brackish or fresh water for growth to maturity. Upon reaching maturity, the American eel migrate back to the ocean to spawn. Spawning occurs in the winter and spring in the Sargasso Sea, and the newly hatched larvae (pre-leptocephalus and leptocephalus stages) passively drift and swim toward the continental shelf where they metamorphose into glass eels (Kleckner and McCleave 1982; Kleckner and McCleave 1985; McCleave et al. 1987).

The transformation from a leptocephalus larvae into a glass eel includes a decrease in body length and weight due to a loss in water concentration, an increase in body thickness, loss of larval teeth, darkening of the eye, changes in the morphology of the head and jaw, and further development of the digestive system (Fahay 1978). Glass eels are miniature transparent American eel that are morphologically similar to elvers (the next life stage), but they are unpigmented. As American eel develop pigment, some begin to migrate into freshwater. These young pigmented American eel are termed elvers. Some elvers remain in coastal rivers and estuaries, while others may continue movements upstream in the winter and the spring (Facey and Van den Avyle 1987). In fact, upstream migration may continue into the yellow- phase for at least three to five years (Haro and Krueger 1991).

The next life stage for American eel is the yellow-phase, which is the primary growth stage where individuals spend most of their lives. The yellow-phase is characterized by a lack of sexual maturity and may last many years. Sexual differentiation begins when eels reach approximately 300 mm TL, primarily during the yellow-phase. Following sexual differentiation, American eel eventually begin to migrate downstream (Krueger & Olivera 1999). Yellow-phase eels gradually metamorphose into silver-phase adults through a process that involves a number of physiological changes. Physiological changes reviewed by Facey and Van den Avyle (1987) include a change in color to a metallic bronze black sheen, pectoral fin color change from yellow-green to black, fattening of the body, thickening of the skin, increased length of capillaries in the rete of the swim bladder, and degeneration of the digestive tract. Additionally, the eyes become enlarged and the visual pigments in the eye are altered (Vladykov 1973; Beatty 1975). These changes are thought to better suit the American eel for migration at deeper depths (Beatty 1975; Kleckner and Kruger 1981; Facey and Van den Avyle 1987). During maturation, American eel migrate downriver to marine waters and out to the Sargasso Sea, where they are thought to spawn once and die (Facey and Van den Avyle 1987).

All American eel comprise one panmictic population, meaning that they are a single breeding population that exhibits random mating. Thus, for example, an American eel from the northern portion of the range could mate with an American eel from the southern portion of the range, and their offspring could inhabit any portion of the range. As a result, recruits to a particular system are likely not the offspring of the adults that migrated out of that system (ASMFC 2000; Avise 2003).

Life history information for American eel remains incomplete, and for some life stages, habitat-specific information is lacking. There is a high degree of uncertainty regarding the range of variation in life history traits that occurs throughout the entire population. Knowledge is lacking on silver eel migration from freshwater to the sea, as well as the egg, leptocephali, and glass eel life stages while in marine waters. Furthermore, while a potential spawning area of the American eel has been hypothesized in the Sargasso Sea, the specific spawning location remains unknown and no spawning activity has been witnessed (ASMFC 2000).

Many studies have indicated that American eel populations are declining (Castonguay et al. 1994 a, b; Haro et al. 2000b). Recent research by Richkus and Whalen (1999, 2000) has shown a decrease in yellow-phase and silver-phase American eel abundance in Ontario, Quebec, New York, and Virginia. For example, during the 31-day peak migration period in 2004, the mean number of American eel passing through the Moses-Saunders Hydroelectric Dam at Cornwall, Ontario, decreased from previous estimates of over 27,000 individuals per day to 274 individuals per day (Casselman *In press*).

Concerns about the decline in American eel abundance prompted a petition in 2004 to list the American eel as endangered under the Endangered Species Act (16 U.S.C. §§ 1531 – 1544). NOAA Fisheries and the United States Fish and Wildlife Service subsequently completed a 12-month status review to determine whether an endangered finding was justified. The findings of the status review indicated that listing the American eel as a threatened or endangered species was not currently warranted due to the fact that American eel are widely distributed and that their overall population abundance remains in the millions. The review also noted that ample historic habitat is available to American eel, and they have the flexibility to complete their lifecycle using marine and estuarine waters, in addition to freshwater. Furthermore, recruitment trends appear to be stable and the factors affecting American eel do not appear to threaten the species at a population level (Federal Register 2007).

Due to their diverse habitat requirements, American eel are subjected to a number of anthropogenic impacts. Fishing pressures and habitat loss are implicated as contributing factors in the American eel decline. Some habitat threats include blockage of stream access, pollution, nearshore habitat destruction, and oceanic changes (Castonguay et al. 1994a, b; ASMFC 2000).

Part A. American Eel Spawning Habitat

Geographical and temporal patterns of migration

American eel are believed to spawn in the Sargasso Sea, which constitutes a large portion of the western North Atlantic Ocean east of the Bahamas and south of Bermuda. Spawning occurs during the winter and the spring, from February to April, and possibly later into the year (McCleave et al. 1987). No other information exists on the spawning requirements, behavior, or exact location of spawning in the Sargasso Sea. Some researchers have speculated that the spawning area is located south of Bermuda and north of the Bahamas in a zone centered at about 25°N and 69°W (Tesch 1977). McCleave et al. (1987) reported spawning in the area from 52ºW to 79°W longitude and 19.5ºN to 29ºN latitude.

Kleckner et al. (1983) and Kleckner and McCleave (1988) hypothesize that within this area, spawning occurs in the subtropical front systems of the oligotrophic subtropical gyres. This frontal zone is located within the North Atlantic Subtropical Convergence and occurs yearly during the time span when spawning is thought to take place. This area separates the warm saline water mass of the southern Sargasso Sea from the lower salinity cool water mass of the northern Sargasso Sea. The area occurs in the upper 500 m of the water column, and it is thought that spawning occurs on the warm side of this front (McCleave and Kleckner 1985; McCleave et al. 1987). However, no direct observations of American eel spawning have been reported anywhere in the world, and no adult American eel have been captured in the Sargasso Sea. Thus, the exact location of spawning area has only been inferred from the collection of leptocephali, or larvae, less than 7 mm in size (Kleckner et al. 1983; Kleckner and McCleave 1985).

The northern limit of the spawning area for American eel appears to be the thermal fronts that separate the northern and southern water masses of the Sargasso Sea (Kleckner et al. 1983). Kleckner et al. (1983) found that the smallest leptocephali collected during their study (3.9 to 5.5 mm) were located on the warm side of these fronts and were rare on the cold side of the fronts. Kleckner and McCleave (1985) suggest that the northern limit for spawning occurs between 24°N and 29°N, and the Bahamas/Antilles Arc forms the southern and western borders. Thus far, the eastern limit of American eel spawning has not been hypothesized (Kleckner and McCleave 1985). Kleckner and McCleave (1985) suggest that this eastern limit may be controlled by a directional orientation mechanism used by American eel adults to locate the spawning area.

It remains unknown how American eel locate the spawning area in the Sargasso Sea and what cues cause them to cease migration. McCleave and Kleckner (1985) offer three hypotheses relating to how American eel migrate in the open ocean. Their first hypothesis is that swimming in one general compass direction (south), in addition to oceanic circulation, allows the American eel to reach the spawning area from anywhere within the species geographical range. Their second hypothesis is that only a moderate directional orientation will result in successful migrations. Their final hypothesis is that migration occurs within the upper three hundred meters of water, which McCleave and Kleckner (1985) speculate is significant with regard to the mechanism of migration. Alternatively, Stasko and Rommel (1977) suggest that American eel orient themselves using geoelectrical fields generated by ocean currents.

Kleckner et al. (1983) suggest that American eel cease migrating when they cross the frontal zone, an area located between 24ºN and 29ºN, which meanders from east to west for hundreds of kilometers. The researchers believe that some feature of the surface water south of the front cues the American eel to cease migration; it may be indicated by a thermal or chemical characteristic of the surface water. In addition, temperature and odor might also serve as cues to halt migration (McCleave and Kleckner 1985). For example, the temperature between the zones may vary as much as 2ºC, and the northern and southern zones exhibit differing species compositions of phytoplankton, zooplankton, and mesopelagic fishes, which could account for a change in odor (McCleave and Kleckner 1985). Furthermore, the upper layers in the pycnocline in the Sargasso Sea may contain dissolved amino acids that are known to be potent to American eel (Liebezeit et al. 1980; Silver 1979). McCleave and Kleckner (1985) suggest it is possible that the leptocephalus larvae imprint to this area in the same way that salmon imprint to a home stream.

American eel are thought to be semelparous, meaning that they die after one spawning event. Evidence for this includes no observations of adult American eel migrating upriver, and no spent adults reported in the literature (Facey and Van den Avyle 1987).

Spawning and the saltwater interface

Salinity might be a key habitat parameter for spawning adult American eel, as spawning is thought to occur on the side of the front in the Sargasso Sea that has warmer temperatures and more saline waters (Kleckner et al. 1983; Kleckner and McCleave 1985). The spawning grounds of the American eel may occur in a high salinity region of the Sargasso Sea where the salinity reaches a maximum of 36.6 ppt (Kleckner and McCleave 1985).

Spawning substrate associations

Bottom composition is not known to be important to spawning adult American eel, as reproduction is thought to occur in the upper 150 to 200 m of the water column (Kleckner et al. 1983; McCleave and Kleckner 1985).

Spawning depth associations

Kleckner et al. (1983) and McCleave and Kleckner (1985) suggest that morphological and physiological evidence indicate that American eel spawning occurs in the upper few hundred meters of the water column. Furthermore, larval American eel (less than 5 mm long) have been located in water 50 to 350 m deep, suggesting that spawning occurs in the upper water column (Kleckner and McCleave 1982).

Spawning water temperature

Temperature may be significant to spawning adult American eel, as they are thought to spawn on the warmer side of the front in the Sargasso Sea (Kleckner et al. 1983; Kleckner and McCleave 1985). Spawning is thought to occur in an area where water temperatures are characterized by 18 to 19°C isotherms between 200 and 300 m (Kleckner et al. 1983). Kleckner and McCleave (1985) describe the hypothesized spawning area as having temperatures greater than 18.2°C. Haro (1991) found that mean preferred water temperature for sexually mature male American eels test in the laboratory ranged between 17.2 and 18.1°C.

Spawning feeding behavior

Once the spawning migration begins, American eel cease feeding and their digestive system atrophies. Gray and Andrews (1971) found no prey and shrunken stomachs in silver eels, suggesting that the subjects ceased feeding before migration.

Spawning competition and predation

Both American eel and European eel (*Anguilla anguilla*) are thought to use the Sargasso Sea for spawning grounds (McCleave et al. 1987). However, McCleave et al. (1987) speculate that American eel spawn from February to April from approximately 19°N to 29°N latitude and 52°W to 79°W longitude, while European eel spawn from March to June from approximately 23°N to 30°N latitude and 48°W and 74°W longitude. Thus, their overlap area may not be significant enough to induce competition.

Part B. American Eel Egg and Larval Habitat

Geographical and temporal movement patterns

Little information exists on the environmental requirements or the incubation period of American eel eggs. It is assumed that the eggs hatch in the same area as they are laid in the Sargasso Sea (see discussion in above section). Hatching is thought to occur from February through April (McCleave et al. 1987), with a possible peak occurring in February (Tesch 1977).

After hatching, American eel undergo a brief pre-larval stage, and then enter the larval leptocephalus life stage. Leptocephali are flattened from side to side and resemble a willow leaf (ASMFC 2000). They grow to between 55 and 65 mm before metamorphosis to the glass eel stage (Kleckner and McCleave 1985). While growing, the leptocephali drift and swim in the upper water column of the open ocean. Their distribution is a result of the oceanic circulation patterns and the swimming behavior of the larvae (ASMFC 2000).

Kleckner and McCleave (1985) reported on the spatial and temporal distribution of leptocephali by collecting specimens and analyzing data collected by Schmidt in the 1920's. They found that leptocephali 7 to 10 mm in length were caught from mid-February to the end of April. In addition, specimens longer than 45 mm were acquired during all months. Kleckner and McCleave (1985) identified two year classes that occurred from February to mid-June: a 0-year class that constituted most samples, and a 1-year class, which represented only a few larvae.

Kleckner and McCleave (1985) collected the majority of leptocephalus larvae between 11°00'N and 42°35'N latitude and 43°50'W and 87°00'W longitude. One 70 mm leptacephalus (a member of the 1-year class) was collected at 49°43'N, 20°45'W. The researchers stated that all leptocephali 10 mm TL or less, and all 0-year leptocephali, were found within a 550 km arc east of the Bahamas and north of the Hispanola Islands. These specimens were found from February to March. Sampling father north and east yielded no leptacephali (Kleckner and McCleave 1985).

From April to May, only one young-of-the-year leptocephalus was collected in the eastern Sargasso Sea from 23°N to 28°N and 51°W to 63°W (Kleckner and McCleave 1985). Kleckner and McCleave (1985) also found young-of-the-year American eel in the Caribbean Current along the western shore of the Yucatan Channel in the Straits of Florida, and in the Gulf Stream to the east of Cape Hatteras, in April and May. Despite the use of nets capable of capturing small leptocephali, no larvae were collected from 38°N to 44°N and 41°W to 55°W in the North Atlantic current (Kleckner and McCleave 1985).

Throughout June and July, young-of-the-year American eel were taken in the Caribbean, Gulf Loop, Florida, and Gulf Stream currents. The samples were taken east to 54°15'W in the southern Sargasso Sea and northeast of Bermuda east to 56°46'W. No larvae were found in the eastern North Atlantic Current at that time. The authors were also unable to define an eastern limit of young-of-the-year larvae during these months in the Gulf Stream due to a lack of collections south of Newfoundland (Kleckner and McCleave 1985).

By August, American eel larvae 40 to 67 mm occupied the entire Gulf Stream area up to the Gulf of Maine. From August through October, only a few large leptocephali, or newly metamorphosed glass eels, remained far out in the Western Atlantic coast (Kleckner and

McCleave 1985). Kleckner and McCleave (1985) reported that during August and September, they collected leptocephali in the southern Caribbean Sea, Gulf Loop Current, Florida Current, Gulf Stream, and North Atlantic Current. Throughout the fall, American eel approached the North American continent and Greenland in the glass eel phase (Kleckner and McCleave 1980; Kract and Tesch 1981). Kleckner and McCleave (1985) found American eel leptocephali in collections in the Caribbean Sea from south of Puerto Rico to the Yucatan Channel in October and November. Likewise, leptocephali were found south of the northeastern United States in October and November, inshore and offshore of the Gulf Stream, and in the Canadian Maritime provinces. However, leptocephali in the south and east in the Sargasso Sea were scarce (Kleckner and McCleave 1985).

Kleckner and McCleave (1985) found that age 1 American eel were scattered widely in collections taken in the Caribbean Sea and western North Atlantic Ocean from February through May. Many specimens were taken near the Bahaman Islands and the Florida Current off the Southeastern United States. They also found metamorphosing American eel leptocephali located north of the Gulf Stream between 65°42'W and 73°30'W, 55 km southwest of Bermuda, and approximately 45 km southeast of Cape Hatteras. One specimen was taken 110 km north of Campeche Bank in the Gulf of Mexico (Kleckner and McCleave 1985).

Larvae are transported northwest from the spawning grounds to the eastern seaboard by the Antilles Current, Florida Current, and the Gulf Stream (Facey and Van den Avyle 1987). The proposed route of American eel larval transport is a westward drift from the spawning grounds in the Sargasso Sea via the Antilles Current, and then moving north with the Florida Current to join the Gulf Stream north of Bermuda (Kleckner and McCleave 1985; McCleave 1993; McCleave et al. 1998).

A small portion of leptocephali reach the Caribbean Sea, Gulf of Mexico, and the Straits of Florida. The proposed route of these larvae occurs to the west and southwest of the spawning grounds via the Windward and Mona Passages, which transport the larvae to the Caribbean Sea. From here, eddies could carry them along the Caribbean coast, or the Caribbean current could convey them through the Yucatan Channel into the Gulf of Mexico and the Gulf loop current (Kleckner and McCleave 1985; McCleave and Kleckner 1987). Leptocephali entering the Straits of Florida are likely carried by the Gulf Loop Current, which flows out of the Gulf of Mexico as the Florida Current. Additionally, they may be conveyed into the Straits of Florida from the Bahamas/Antilles archipelago by currents through the Old Bahama Channel, then the Nicholas and Santaren Channels north of Cuba, or through the Northwest Providence Channel south of Grand Bahaman Island (Kleckner and McCleave 1985).

It is possible that some eel larvae become trapped in the Sargasso Sea for over a year by recirculating currents (Knights 2003). This occurs when the larvae become trapped in the sub-gyre where the Florida and Antilles Currents interact, thus causing the larvae to drift north, or recirculate back into the oligotrophic Sargasso Sea from the Gulf Stream (Boëtius and Harding 1985).

As the larvae approach the edge of the continental shelf, they metamorphose into miniature transparent eel, called glass eels (Kleckner and McCleave 1985). This occurs by early October when the American eel are between 55 mm and 65 mm (Kleckner and McCleave 1985).

Eggs, larvae, and the saltwater interface

The salinity requirements of eggs and larvae have not been documented in literature. Facey and Van den Avyle (1987) state that post-larval American eel are tolerant of a broad range of salinities because they occur both in freshwater and marine habitats. Additionally, leptocephali are in near-ionic equilibrium with seawater (Hulet et al. 1972).

Egg and larval substrate associations

Bottom substrate is not important to this lifestage, as American eel larvae are planktonic and float and drift in the water column. Thus, no bottom substrate is used during this life stage (Kleckner and McCleave 1985).

Egg and larval depth associations

The importance of depth to the American eel egg stage is not stated in the literature. No information exists on the depth that eggs are found, as they have never been collected in the Sargasso Sea (ASMFC 2000).

Once American eel enter the leptocephalus stage, they are found in the upper 250 m of the water column (Castonguay and McCleave 1987). Larvae less than 5 mm long have been captured at depths between 50 m and 350 m. Furthermore, larvae between 5 and 10 mm appear to vertically migrate, as they are found between 100 m and 150 m during the day and between 50 m and 100 m at night. (Castonguay and McCleave 1987; McCleave et al. 1987).

Egg and larval water temperature

No studies have concluded the egg and larval temperature requirements of American eel in the wild. However, Japanese eel (*Anguilla japonica*) eggs hatch in 38 to 45 hours at 23°C (Yamamoto and Yamauchi 1974). Spawning and hatching is likely to occur on the warm side of the front in the Sargasso Sea where temperatures are greater than 18.2°C (Kleckner and McCleave 1985).

Egg and larval competition and predation

Both American and European eel use the Sargasso Sea as a spawning ground. As a result, the youngest stages of both eel species may share a small portion of the same habitat. However, Kleckner and McCleave (1985) state that while there is an overlap in range, competition does not occur. American eel larvae are predominately found west of 62°W and south of 25°N, while European eel are located in a different area (Kleckner and McCleave 1985; McCleave and Kleckner 1987).

One study by Appelbaum (1982) suggests that predation on American eel larvae in the Sargasso Sea may be minimal. Researchers found that of 1,000 pelagic fish representing 25 species, only the myctophid, *Ceratoscopelus warmingii*, had American eel leptocephali in its stomach. This suggests that American eel may spawn in a nutritionally poor area, thus increasing the chance of survival due to a lack of predation. However, more research is needed to fully explore the issue (Appelbaum 1982).

Part C. American Eel Elver (including Glass Eel) Habitat

Geographical and temporal movement patterns

American eel metamorphose from leptocephalus larvae to glass eels over the Continental Shelf. Shortly after metamorphosis, the unpigmented glass eels enter estuaries, eventually migrate to freshwater, and ascend rivers during the late winter and early spring. It is thought that glass eels and elvers use olfaction to locate freshwater (Sheldon 1974; Sorensen 1986; Sorensen and Bianchini 1986); however, the specifics of this theory are mostly unknown. For example, Sorensen (1986) reported that American eel were attracted to the smell of brook water, as well as the smell of leaf detritus. Furthermore, Creutzberg (1959, 1961) demonstrated that European eel were able to detect the odor of freshwater, and alter their behavior accordingly.

Vladykov (1966) stated that the American eel migration upriver occurred earlier in the southern portion of the range than in the north. However, other studies showed variations and overlaps in migration timing (Facey and Van den Avyle 1987). Migrating American eel in the Southeastern states and the Mid-Atlantic have been collected from January through May (Jeffries 1960; Smith 1968, Fahay 1978; Hornberger 1978; Sykes 1981; Helfman et al. 1984). In the Northern states, migrating glass eels reach estuaries as early as late winter (Jeffries 1960), although the main migration occurs in the spring. In the East River, Chester, Nova Scotia, Jessop (2000) reported eel recruitment in the river mouth from May through June, and upstream migrations from July through September. Dutil et al. (1989) reported that the glass eel and elver migration to the St. Lawrence estuary occurred in the second half of June and was finished by the end of July.

Slightly south, American eel in Maine were documented arriving upstream from the end of March to the beginning of May (Facey and Van den Avyle 1987). Ricker and Squires (1974) and Sheldon (1974) reported that American eel ran in Maine from late April to June. In Rhode Island, migrations peaked during April and May (Facey and Van den Avyle 1987). Further south, in North Carolina, Rulifson et al. (2004) found that recruitment of elvers occurred from January through April, with the highest density of American eel present from March to April.

Glass eels enter estuaries by drifting on flood tides and holding position near the bottom of ebb tides (McCleave and Wippelhauser 1987), and by actively swimming along shore in estuaries above tidal influence (Barbin and Krueger 1994). Movements of glass eels are primarily nocturnal (Dutil et al. 1989). Eventually, glass eels in estuaries change into pigmented elvers (Haro 1991).

Throughout the elver life stage, American eel are mostly active at night. During the day elvers either burrow or remain in deep waters (Deelder 1958). Elvers move back up into the water column on flood tides and return to the bottom during ebb tides (Pacheco and Grant 1973; McCleave and Kleckner 1985; McCleave and Wippelhauser 1987).

Documentation shows that American eel stall their inward migration before they enter freshwater (McCleave and Kleckner 1985). The cues that trigger this behavior are unknown. Some researchers hypothesize that American eel may be able to detect the odor of freshwater (Creutzberg 1959, 1961; Sorensen 1986). Stalling at the freshwater interface may allow individuals to adjust physiologically and behaviorally before entering the new environment (Sorensen and Bianchini 1986). This upstream migration is possibly triggered by water chemistry changes associated with the intrusion of estuarine water during the high spring tides (Sorensen and Bianchini 1986).

Elvers eventually begin their upstream migration and become more active during the day (Sorensen and Bianchini 1986). Tesch (1977) reported that European elvers oriented themselves with river currents for upstream movement. If the current was too weak or strong, the European eel moved into backwater areas and delayed migration. Since American eel and European eel have similar behavior patterns, it is possible that fast or slow currents also affect American eel (Tesch 1977).

Factors that are thought to influence the daily abundance of migrating elvers include nightly tidal height, river water temperature and discharge, and the difference between bay and river temperatures (McCleave and Kleckner 1985; Sorensen and Bianchini 1986; Ciccotti et al. 1995; McCleave and Wipplehauser 1987; Wipplehauser and McCleave 1987; Martin 1995; Jessop 2003). Migration occurs in waves and is initially triggered by an increase in temperature to between 12 and 14°C. After initiating migration, temperature does not appear to have a functional influence on migrating elvers (Jellyman and Ryan 1983; Martin 1995; Jessop 2003). River discharge appears to control the daily abundance of upstream migrants, with decreases in abundance coinciding with increases in river discharge. Jessop (2003) stated that increased tidal height delivered an increased abundance of elvers to the river mouth. Temperature then triggered upstream migration, while discharge controlled the rate of movement upstream (Jessop 2003).

While most American eel elvers migrate into freshwater, some may cease migration in coastal waters and estuaries and remain there from the time they arrive until they reach the mature silver eel stage and begin the spawning migration (Morrison et al. 2003, Lamson et al. 2006). In addition to the upriver migration, fall and spring migrations have been documented (Smith and Saunders 1955; Medcof 1969).

Elvers and the saltwater interface

Little is known about the salinity requirements of juvenile American eel. Sheldon and McCleave (1985) documented glass eels in Penobscot, Maine, in salinities ranging from 0 to 25.2 ppt.

Elver substrate associations

Substrate may be an important habitat parameter for juvenile American eel, as elvers have been seen burrowing during the day and in between movements upstream. American eel appear to use many different types of substrates. Facey and Van den Avyle (1987) stated that migrating elvers make use of soft undisturbed bottom sediments as shelter. Furthermore, a study by Edel (1979) demonstrated that American eel are less active when there is shelter present. Fahay (1978) stated that post-larval American eel are benthic and utilize burrows, tubes, snags, plant masses, other types of shelter, and the substrate itself. Additionally, American eel have been documented burrowing in both mud and sand (P. Geer, Georgia Department of Natural Resources, personal communication). Elvers may also use the hydraulic boundary layer of rough substrates to facilitate migration upstream, or migrate through interstitial spaces within a substrate to avoid high water velocities during upstream migration (Barbin and Krueger 1994).

Elver depth associations

Creutzberg (1961) reported that at night, unpigmented European eel in coastal waters were found in a variety of depths throughout the water column during incoming tides. During the day, elvers move to the bottom and bury themselves in the substrate (Deedler 1958).

Elver water temperature

Temperature is important to elvers because it is thought to trigger upstream migration. Migrations of American eel begin when the temperature rises above 10ºC, with the majority of movement occurring at temperatures greater than 20ºC (Moriarty 1986; Haro and Krueger 1991; Richkus and Whalen 1999; Jessop 2003). Jessop (2003) found that elvers in the East River, Chester, Nova Scotia, actively moved upstream when river temperatures reached 10 to 12°C, and the first wave of migrants peaked at 11 to 16°C. Water temperatures of less than 10°C had a gating effect on the elvers (Jessop 2003).

Other researchers have found similar results. Helfman et al. (1984) noted migrations in Georgia at 11°C, Soreson and Bianchini (1986) found a range of 10 to 15°C in Rhode Island, with a peak at 14°C, and Smith (1955) and Groom (1975) found a temperature range of 10 to 12°C for migrating American eel in New Brunswick. While temperature is thought to play an active role in stimulating migration, other factors also play a role in the abundance of American eel migrating upstream (Jessop 2003).

Beyond stimulating migration, temperature does not appear to play a key role in the elver life cycle. Juvenile American eel utilize a broad range of habitats and are likely to have flexible temperature tolerance ranges. Glass eels were documented in Penobscot, Maine, in temperatures ranging from 3.9 to 13.8ºC (Sheldon and McCleave 1985). Elvers have been documented in a wide variety of temperatures, including cold freshwater streams and lakes, and warm brackish coastal bays and lakes. In fact, elvers have been found at temperatures as low as -0.8°C in the Narragansett Bay, Rhode Island (Jeffries 1960).

Elver water velocity/flow

Sheldon and McCleave (1985) noted that in Penobscot, Maine, glass eels accumulated on the surface when surface currents on the ebb tide decreased below 15 $cm \cdot s^{-1}$. In another study, river discharge and its effects on water velocity were found to be the primary factor influencing the rate of elver upstream migrations (Jessop 2000). In velocities exceeding 35 to 40 $cm \cdot s^{-1}$, elvers had difficulty swimming and maintaining their position (McCleave 1980; Barbin and Krueger 1994). Jessop (2000) found that most elvers would not swim at water velocities exceeding 25 $cm \cdot s^{-1}$, and instead would remain resting in the substrate. Some researchers have found that delays or prevention of upstream elver migration can be caused by high flows (Lowe 1951; Jessop and Harvie 2003). Similarly, Lowe (1951) noted that high flows on the Bann River, Ireland, delayed European eel (*A. Anguilla*) elver migrations for many weeks.

Elver feeding behavior

Dutil et al. (1989) found that the stomachs of elvers contained 90% *Chironomidae* and 8% *Simuliidae*. No food remains were found in the stomachs or intestines of glass eels (Dutil et al. 1989).

Glass eel competition and predation

Glass eels are preyed upon by many fish species including striped bass. American eel were found in 20% of striped bass stomachs in the Merrimack River, New Hampshire. Additionally, migrations of striped bass coincide with upstream elver migrations (reviewed in Richkus and Whalen 1999). Jessop (2000) found that a major source of predation on American eel elvers in the East River, Chester, Nova Scotia, was cannibalism by larger individuals of the same species. Other authors have also reported cannibalism on younger American eel (Tesch 2003).

Part D. Yellow-phase American Eel Habitat

Geographic and temporal movement patterns

Some yellow-phase American eel continue migrating upstream until they reach maturity, while others remain in the lower portions of coastal estuaries and rivers (Morrison et al. 2003; Cairns et al. 2004; Lamson et al. 2006). Morrison et al. (2003) studied the migration histories of yellow eels using otolith microchemistry. Yellow eels in the Hudson River, New York, showed three modes of habitat use: 1) the freshwater mode, in which yellow eels and elvers utilized only freshwater habitats; 2) the mixed mode, where American eel resided in freshwater for at least 2 years before migrating back to brackish water; and 3) the brackish mode, where American eel remained entirely in brackish habitats, without ever utilizing freshwater environments (Morrison et al. 2003). Individuals that exhibited the brackish mode had increased growth rates, earlier maturation, and began their downstream migrations sooner than those that utilized freshwater habitats (Morrison et al. 2003; Cairns et al. 2004; Lamothe et al. 2000). These findings support the Helfman et al. (1987) hypothesis that brackish water habitats are more productive than freshwater for American eel.

Lamson et al. (2006) also used microchemistry to trace movements of American eel in Prince Edwards Island, Canada. Findings of this study showed that 69% of individuals moved between salt and freshwater. Half of the freshwater American eel sampled showed freshwater residency only. The authors state that this may have been due to distances to other salinity zones or dams that impede movements. American eel were also found to be able to complete their lifecycle entirely in brackish water habitats (Lamson et al. 2006). Other research (Thibault et al. 2007) indicates that movements between freshwater and estuarine zones may be regular and seasonal in nature, as a response to low winter temperatures in the estuary.

Movement of yellow eels and upstream migrations occur primarily at night from dusk to dawn. However, movement does sometimes occur during the day (Dutil et al. 1988; McGrath et al. 2003c; Verdon et al. 2003). Some studies have indicated that American eel migrate in response to the lunar cycle, with individuals being less active during moonlit periods (Sorensen and Bianchini 1986; Cairns and Hooley 2003; Hildebrand 2005). Other studies indicate that high tides and increased river flow may increase movements (Dutil et al. 1988; Hildebrand 2005). Dutil et al. (1988) found that American eel moved upstream during high tides and were more than two times as active during high tides compared with low tides.

Yellow eels remain in freshwater and brackish systems for up to 30 years before maturing into silver eels and migrating to the sea to spawn (Tesch 1977; Helfman et al. 1987; Able and Fahay 1998). Few young American eel are found in inland lakes (Hurley 1972; Facey and LaBar 1981); migrants to farther reaches upstream tend to be older, larger, more mature females (Helfman et al. 1987; Haro and Krueger 1991; Oliveira 1999; Morrison et al. 2003).

American eel migrations upstream occur from March through October, and peak in May and July depending on location (Richkus and Whalen 1999). McGrath et al. (2003c) found that the numbers of American eel in the St. Lawrence River, New York, approaching the Moses-Saunders Power Dam peaked in early July and early October. Verdon et al. (2003) found that American eel in the Richelieu River, Quebec, began upstream migrations as early as June 11th and ended in late September. Hildebrand (2005) found that in the Shenandoah River, West

Virginia, American eel utilized the eel ladder at Millville Dam from March through October (the duration of time that the ladder was installed).

There is substantial evidence that some American eel establish a home range (Table 7-1). A home range is defined as the spatial extent or outside boundary of an animal's movement during the course of its everyday activities (Burt 1943). The size of the home range can be influenced by food availability, competition, and predator density (Bozeman et al. 1985). Ford and Mercer (1986) found some evidence of a home range and territoriality, and found that larger American eel were located primarily in large creeks, while smaller American eel were found in narrow creeks at the back of the marsh, in the Great Sippewisset Marsh, Massachusetts. They found that 93% of the American eel in their study traveled less than 100 m (Ford and Mercer 1986).

Citation	Home Range	Method	Waterbody Type
Ford and Mercer 1986	0.0209 ha	Areal analysis	Tidal creek
Dutil et al. 1988	0.5 – 2.0 ha	Linear distance	Tidal river
Parker 1995	~325 ha	Areal analysis	Tidal estuary
Gunning and Shoop 1962	<137 m	Mark-recapture	Estuary
Helfman et al. 1983	~1 ha	Polygons	Estuarine stream
Oliviera 1997	Max 4.7 km	Mark-recapture	River
Morrison and Secor 2003	Max 4.2 km	Mark-recapture	River
La Bar and Facey 1983	2.4 – 65.4 ha	Displacement polygons	Bay/lake
Thomas 2006	3 ha (18 ha)	50% (95%) kernels	Impounded lake

Table 7-1. Yellow-phase American eel home range estimates (adapted from Thomas 2006)

Parker (1995) found that homing in yellow-phase American eel in the Penobscot Estuary, Maine, was precise. More than half of the displaced American eel returned to within 300 m of their capture site, and three American eel moved towards their capture sites, but did not arrive there while under observation. Some of the American eel returned to within 50 m of the capture site and remained there for several days, indicating that the American eel returned to a specific area and not just a general location. In another study, Lamothe et al. (2000) found that American eel returned to home ponds after being moved to an adjacent pond.

Morrison and Secor (2003) also found that American eel in the Hudson River established a home range. They found that more than 70% of their PIT tagged American eel moved less than 1 km from the original tagging area in a 2 to 12 month time period. The longest dispersal was 4.2 km from the tagging site. However, the authors did suggest that based on otolith microchemistry, some American eel may have dispersed in the estuary over longer time periods (Morrison and Secor 2003).

Habitat influence on sexual differentiation

Many studies indicate that sex ratios of American eel are highly variable. This occurs both regionally and within individual systems (Hansen and Eversole 1984; Helfman et al. 1984). Hansen and Eversole (1984) found that females dominated males 23 to 1 in the Cooper River, South Carolina. Helfman et al. (1984) found that 36% of the American eel in a Georgia estuary were male, while only 6% of American eel in freshwater were male. Goodwin and Angermeier (2003) determined that while presence of male American eel in the Potomac River tributaries ranged from 0 to 100%, in the mainstem river 29% of individuals were male. Furthermore, 100% of the American eel in the Shenandoah River were female (Goodwin and Angermeier 2003). Further north, Oliveira et al. (2001) found that 49% to 98% of American eel in the Chandler, East Machias, and Sheepscot Rivers, Maine, were male. Additionally, females have been reported as dominant in most Canadian habitats (Gray and Andrews 1971; Dolan and Power 1977; Jessop 1987).

Various hypotheses have been developed to explain the skewed sex ratios. Vladykov (1966) hypothesized that females were found predominately in higher latitudes, while males were found in lower latitudes. However, Krueger and Oliveira (1997) and Oliveira et al. (2001) found the opposite. Krueger and Oliveira (1997) found that males outnumbered females 3 to 1 in the Annaquatucket River, Rhode Island. In addition, Oliveira et al. (2001) found that males made up 0% to 98% of the population within a single degree of latitude between Maine and Nova Scotia rivers.

Another theory is that female American eel are found in freshwater, while males are found in estuaries (Vladykov 1966; Tesch 1977). However, Winn et al. (1975) contradicted this hypothesis when they found more males in freshwater habitats and more females in estuaries in Rhode Island. Alternatively, Helfman et al. (1987) suggested that males were found in estuaries because these productive habitats led to fast growth. Females, on the other hand, preferred freshwater habitats that led to slower growth and increased fecundity (Helfman et al. 1987).

Helfman et al. (1987) also proposed that females delayed metamorphosis until they reached areas of higher latitude. However, Oliveira et al. (2001) found high variation in the proportion of males along a 30 km stretch of the Chandler, East Machias, and Pleasant Rivers in Maine, suggesting that delayed metamorphosis by females was unlikely.

Oliveira et al. (2001) also found that the proportion of males was inversely related to the amount of available lacustrine habitat; this finding was independent of distance inland. American eel from lacustrine habitats were found to be female, while samples from fluvial habitats were mostly male. The researchers concluded that river habitat may affect the distribution of sexes and play a role in sexual determination (Oliveira et al. 2001).

Other evidence suggests that density of American eel plays the key role in determining the sex of an individual; males are produced in high density areas, and females in low density areas. Thus, females are more common in upper reaches of rivers where density is lowest (Krueger and Oliveira 1999). Oliveira (1999) and Oliveira et al. (2001) hypothesize that males are produced in areas where crowding is occurring. Furthermore, males favor areas closer to the sea and spawning ground in more productive habitats, where they can grow and mature faster (Helfman et al. 1987). On the other hand, females tend to disperse widely within their range and utilize all suitable habitats. They favor slower growth and greater size, thus increasing fecundity and swimming ability (Krueger and Oliveira 1999; Goodwin and Angermeier 2003). In fact, in upper reaches of rivers, American eel tend to mature at older ages and larger sizes (Helfman et al. 1987).

Yellow eels and the saltwater interface

Salinity is not likely a key habitat parameter for American eel, as they are found in a wide range of salinities (Morrison et al. 2003). Geer (2003) reported that in the Chesapeake Bay, Virginia, more American eel were present in the upper tributaries near or above the saltwater interface. Eighty-nine percent were caught in salinities below 12 ppt, and 27% of the catch occurred in waters less than 2 ppt (Geer 2003). Additionally, Dutil et al. (1988) found that American eel selected salinities less than 12 ppt in areas where mid-channel salinity levels reached 24 ppt.

While American eel do not, in general, seem to select habitats based on salinity, it may influence growth rates. Morrison et al. (2003) found that yellow eels that showed evidence of freshwater residency had slower growth rates than those that spent their entire lives in brackish water. Brackish water habitats are thought to have higher food abundances, better quality food, lower predation pressure, and less thermal and osmotic stress. Helfman et al. (1987) suggested that productivity was higher downriver in brackish habitats as compared to upriver habitat. Yellow eels in brackish water are thought to grow faster, mature earlier, and migrate downstream as silver eels sooner. Freshwater habitats are thought to lead to later maturation and overall larger individuals (Helfman et al. 1987).

Yellow eel substrate associations

Yellow-phase American eel are bottom/substrate oriented and may show little movement, particularly during the day (Eales 1968; Ogden 1970; Tesch 1977; LaBar and Facey 1983; Helfman 1986). However, the substrate preference of American eel is not well documented in the literature. LaBar and Facey (1983) reported that American eel in Lake Champlain were found over weedy bottoms. Ford and Mercer (1986) documented small American eel in soft-bottomed creeks of landward marshes, and larger American eel in soft mud to sandy-bottomed creeks of seaward marshes. Geer (2003) found that in the Chesapeake Bay, Virginia, American eel were mostly found over detritus, hydroid, or shell bottoms. Chaput et al. (1997) state that American eel in the St. Lawrence River use soft sediments to burrow during the winter.

Thomas (2006) suggested that riparian vegetation and complex substrate were important to yellow-phase American eel in impounded systems. Additionally, American eel were more likely to be found in areas with coarser substrates (i.e., sand, gravel, or rock) in the morning-afternoon, and winter-spring because individuals were less active and seeking shelter during those times. However, during comparatively more active times (i.e., evening-night and summer-fall) in an impounded system, American eel were more likely to be in areas with finer substrates (i.e., silt or clay) (Thomas 2006).

Yellow eel depth associations

Little information exists regarding the depths at which American eel are found. Due to the diverse range of habitats that American eel utilize, depth range probably varies greatly. Facey and LaBar (1981) found American eel in water 1 to 2 m deep. Geer (2003) found that the majority of yellow eels were caught in the upper tributaries of the Chesapeake Bay in depths of 4 to 10 m.

Thomas (2006) found that yellow-phase American eel in an impounded system typically occupied depths of 0.4 to 1.5 m (available depths of 0 to 2.93 m). In addition, while mean morning (1.1 m) and afternoon (1.1 m) depths were relatively shallow, mean evening (1.3 m) and night (1.4 m) depths were slightly deeper. Given the relatively shallow nature of the impounded system, these changes in depth usually represented areas with different substrate and variable distances from shore. Furthermore, mean winter (0.8 m) and spring (0.9 m) depths showed use of shallow habitat, while mean summer (1.2 m) and fall (1.3 m) depths showed use of deeper areas. Therefore, American eel utilization of different depth areas may be dependent upon time of day and season (Thomas 2006).

Yellow eel water temperature

Researchers hypothesize that the onset of upstream migration in yellow eels is linked to water temperature (Moriarty 1986; Haro and Krueger 1991; EPRI 1999). Knights and White (1998) found that European eel were stimulated to migrate by temperatures greater than 14 to 16°C, and increases in migrations occurred at temperatures greater than 20°C. Similarly, Verdon et al. (2003) determined that migration occurred earlier in the Richelieu River, Quebec, than in the upper St. Lawrence River. The St. Lawrence is a larger lake-fed system that has more gradual and less variable temperature increases than the Richelieu system; the researchers hypothesized that this pattern might cause a delayed upstream migration (Verdon et al. 2003). In the upper St. Lawrence River, upstream migration begins in late June and peaks at the end of July (Verdon and Desrochers 2003).

Verdon and Desrochers (2003) found that captures of American eel in the St. Lawrence River peaked when temperatures reached 22 to 23°C, and decreased as water temperatures dropped from 24°C to 21°C. Once the temperatures fell below 21°C, captures of American eel became scarce (Verdon and Desrochers 2003). McGrath et al. (2003c) noted a decrease in migrant yellow eels at the Moses-Saunders Power Dam in the St. Lawrence River, when temperatures declined to 10°C in the fall. Additionally, Geer (2003) reported that American eel in the Chesapeake Bay, Virginia, were found between 13°C and 27°C. They were most abundant in waters where the temperature was 26 to 28°C and least abundant in waters less than 8°C. Low catch rates at these temperatures suggested inactivity. However, researchers found no direct correlation between temperature and catch, although peaks seemed to coincide with increased temperature (Geer 2003). Haro (1991) determined the range of preferred temperatures for yellow eels in a freshwater laboratory was between 17.8 and 19.8°C.

Yellow eels live in a variety of habitats, including cold, high-elevation or high-latitude freshwater streams and lakes, to warm, brackish coastal bays and estuaries in the Gulf of Mexico (Facey and Van den Avyle 1987). American eel have been reported to survive passage through a nuclear power plant, where they were exposed to elevated temperatures for 1 to 1.5 hours (Marcy

1973). Furthermore, American eel are thought to become torpid at temperatures less than 10°C. Walsh et al. (1983) held yellow eel at 5°C for over five weeks, and found that at temperatures less than 8°C they stopped feeding and remained inactive for months.

Yellow eel dissolved oxygen associations

Rulifson et al. (2004) found that catch of American eel was affected by dissolved oxygen rates, and determined that dissolved oxygen was a strong predictor of the distribution of American eel in North Carolina. High catches of American eel were almost always in waters with dissolved oxygen levels above 4 mg/L (Rulifson et al. 2004). Similarly, Geer (2003) found that 82% of the American eel caught in the Chesapeake Bay, Virginia, were found in waters with dissolved oxygen levels between 5 and 9 mg/L. However, no association was found between dissolved oxygen and catch (Geer 2003). This could be due to the fact that sampling was conducted only in the areas with dissolved oxygen levels above 5 mg/L (Rulifson et al. 2004).

Yellow eel water velocity/flow

Yellow eels are likely not water velocity dependent, as high densities of American eel have been found in lakes and ponds where velocity is low or nonexistent (K. McGrath, New York Power Authority, personnel communication). However, Wiley et al. (2004) found that in Maryland, velocity-depth diversity was the only stream habitat variable related to American eel density. The highest densities of eel occurred in sites that had four velocity-depth regimes: slow (<0.3 m/s)-deep (>0.5 m/s), slow-shallow (<0.5 m/s), fast (>0.3 m/s)-deep, and fast-shallow. Sites with only one of two velocity-depth regimes had significantly lower American eel densities (Wiley et al. 2004).

Yellow eel feeding behavior

The yellow eel phase is the feeding and growth stage for the American eel. American eel are thought to be opportunistic feeders, preying upon whatever is available in their habitat (Colette and Klein-MacPhee 2002). American eel can feed heavily on demersal fish eggs, larvae, and juveniles (Knotek and Orth 1998). Mature American eel have been documented feeding on invertebrates including insects, crayfish, snails, worms, and small fish (Ogden 1970; Scott and Crossman 1973; Facey and LaBar 1981). They have also been documented consuming plant material (Moriarity 1978) and carrion (Ogden 1970). Additionally, cannibalism on smaller conspecifics has been documented in the literature (Domingos et al. 2006).

Godfrey (1957) found that 90% of the American eel's diet consisted of insects, while 10% consumed whole fish. Facey and LaBar (1981) reported that American eel feed heavily upon benthic organisms. They found that 43% of stomachs contained insects, 26% contained fish and crayfish, and 20% contained gastropods. The rest of the stomachs were empty. The authors noted that American eel in this study consumed fish more than in other studies, and suggested that yellow eels in Lake Champlain, Vermont, relied more on fish due to their large sizes (Facey and LaBar 1981). In another study, Wenner and Musick (1975) documented American eel preying heavily on blue crabs (*Callinectes sapidus*) and bivalves (*Mya arenaria*, *Mulinia lateralis*, and *Macoma* spp.) in the James, York, and Rappahannock Rivers, Virginia. They also found that American eel preyed upon alewife (Wenner and Musick 1975).

Denoncourt and Stauffer (1993) found that American eel in the Delaware River fed on 56 taxa, including 4 fish species and 52 macroinvertebrates. Macroinvertebrates were found in 98.8% of the feeding American eel. Mayflies (Ephemeroptera) and stoneflies (Plecoptera) made up 69% of the prey items, followed by caddisflies (Trichoptera, 33.9%), beetles (Coleoptera, 23.4%), flies (Diptera, 16.4%), fishflies and hellgrammites (Megaloptera, 12.8%), and dragonflies and damselflies (Odonata, 11.1%). Fish species were found in 7% of the feeding American eel and included lamprey ammocetes (*Petromyzon marinus*), madtoms (*Noturus insignis*), and minnows (*Notropis* sp.). Other items in the stomachs included detritus and vegetation, bones and flesh, and sand and gravel (Denoncourt and Stauffer 1993).

Lookabaugh and Angermeier (1992) also found that prey size increased with the size of the American eel. In the piedmont regions of the James River drainage (Virginia), small American eel fed primarily on aquatic insects, whereas larger American eel consumed fish and crayfish (Decapoda). In the coastal plain, small and medium sized American eel preyed upon microcrustaceans and aquatic insects, while large American eel fed on crayfish. Similarly, Ogden (1970) determined that smaller American eel (less than 40 cm) in New Jersey streams mostly fed on aquatic insect larvae, including Ephemeroptera, Megaloptera, and Trichoptera, while the larger American eel consumed fish and crustaceans. Smith (1985) also reported smaller American eel feeding on mayflies, magalopterans, and caddisflies. In addition, Rulifson et al. (2004) found that in North Carolina, large American eel consumed crayfish and fish (mullet and centrarchids). Smaller American eel fed on arthropods, small mullet and minnows, polychaetes, unidentifiable matter, and plant material. Fish, crustaceans, and arthropods were the most important prey items (Rulifson et al. 2004).

In addition, Sorensen et al. (1986) reported that in Rhode Island American eel fed primarily at night, with activity peaking at nightfall.

Part E. Silver American Eel Habitat

Geographic and temporal patterns at sea

Once American eel enter their final life stage, termed silver-phase, the maturation process accelerates and they migrate out to the Sargasso Sea to spawn. In New England tributaries, spawning migrations begin in the late summer and continue through fall. American eel migrate later in the Southeastern states and in the Mid-Atlantic than in the Northern states. It is hypothesized that this delay helps to synchronize the arrival of the American eel at the spawning grounds in the Sargasso Sea (Wenner 1973; Facey and Helfman 1985; Helfman et al. 1987).

Yellow eels transform into silver eels before migrating out to sea. Little is known about this final phase of their life history (ASMFC 2000). Downstream migrations occur in sudden bursts with long periods of no movement and peaks of intensive movements (Barbin et al. 1998). The rate of migration varies, with pauses occurring while the silver eels wait for specific environmental cues (Richkus and Whalen 1999).

Silver eel migration begins at different times of year depending on location, but occurs primarily in the fall, although winter migrations have been documented (Facey and Helfman 1985; Euston et al. 1997, 1998). In Newfoundland, the largest American eel migrations occur in late September and early October (Bouillon and Haedrich 1985). McGrath et al. (2003a) found that American eel in the upper portion of the St. Lawrence River migrated downstream from the end of June to the beginning of October, and that the primary migration in the lower estuarine portion of the river occurred in October. Slightly south, Winn et al. (1975) documented American eel migrating in Rhode Island from September through November.

Migration of mature American eel is thought to occur mostly at night (Winn et al. 1975; Haro et al. 2000a; McGrath et al. 2003b). Haro et al. (2000a) stated that silver eels in the Connecticut River, Massachusetts, migrated primarily at night within several hours after sunset, and became inactive during the day. The variables thought to influence downstream migration of silver eels include water temperature, river and stream discharge, odor, and light-intensity, including moon phase (Hain 1975; Westin 1990; Haro 1991; Richkus and Whalen 1999; Richkus and Dixon 2003). In fact, research has indicated that catch rates of American eel are higher during the dark phases of the moon and when cloud cover is highest (Winn et al. 1975; Cairns and Hooley 2003; McGrath et al. 2003b). Cairns and Hooley (2003) found that in tidal bays and estuaries in Prince Edward Island, Canada, catch per unit effort (CPUE) for silver and yellow eels decreased at full moon. CPUE was negatively correlated with the proportion of moon fullness and was negatively correlated with the illuminance index (Cairns and Hooley 2003). Cairns and Hooley (2003) suggest that this is a mechanism to avoid predation. Furthermore, some studies indicate that American eel exhibit an endogenous lunar cycle of activity (Boëtius 1976; Hain 1975; Edel 1976).

Rainfall, which leads to increased river discharge, may also have an impact on silver eel migrations (Lowe 1951; Winn et al. 1975; Charles Mitchell & Associates 1995; Euston et al. 1997, 1998). Winn et al. (1975) noted increased migrations after rains, as well as during the third and fourth lunar quarter. Haro et al. (2003) found in Maine that more American eel were captured on, or soon after, days with rain than on dry days.

The age and size at which migration begins varies geographically. American eel in the northern part of the range exhibit slower growth and remain longer in freshwater and estuarine systems before beginning migration back to sea (Facey and LaBar 1981). Various studies in Newfoundland, Lake Ontario, and Lake Champlain have shown that American eel migrate back to sea after about 12 to 13 years, and at a mean size of 69 cm (Gray and Andrews 1971; Hurley 1972; Facey and LaBar 1981; McGrath et al. 2003a). In the southern part of their range, American eel begin migrating earlier than in the north (Hansen and Eversole 1984; Helfman et al. 1984; Owens and Geer 2003). Hansen and Eversole (1984) found that in the Cooper River, South Carolina, American eel older than 7 years old and greater than 65 cm in length were sparse, suggesting that adults migrate at a younger age and smaller size. Helfman et al. (1984) found similar results in the Altamaha River, Georgia. More recently, Owens and Geer (2003) found that populations in Virginia tidal rivers were comprised mostly of American eel less than 7 years old, indicating that migrations had occurred by this age.

Silver eel salinity associations

The importance of salinity to silver-phase American eel has not been documented in the literature. As a habitat generalist, American eel utilize a wide variety of salinities from freshwater to saltwater, thus migrations occur through a broad range of salinities. Barbin et al. (1998) suggested that changes in salinity could be used as a mechanism to help orient American eel out of estuaries. These researchers documented American eel in the Souadabscook stream (tributary to the mouth of the estuary) and the Penobscot Estuary, Maine, in salinities ranging from 0 to 30 ppt (Barbin et al. 1998).

Silver eel substrate associations

There is little information documented in the literature on the substrate requirements of silver-phase American eel. One study by Valdykov (1955) reported that silver eels in the northern habitats utilized muddy substrates during the winter months. Goodwin and Angermeier (2003) found that the highest catch of American eel in Shenandoah River drainages appeared to be associated with site characteristics including leaf packs, rootwads, woody debris, and flowing water.

Silver eel depth associations

Depth does not appear to be an important habitat characteristic for silver-phase American eel, as authors have documented use of a wide range of depths during outmigrations. Haro et al. (2000a) found that silver eels in a hydroelectric forebay on the Connecticut River, Massachusetts, used many depths, but occupied depths most frequently between 6.6 and 10 m. However, American eel were also observed swimming at night near the surface of the water (Haro et al. 2000a). Similarly, McGrath et al. (2003b) found, during their surface and midwater trawling study, that American eel were caught at the highest rates between 6 and 10 m. However, the researchers stated that they were unsure if these findings were significant since sampling was limited near the bottom (between 18 and 24 m) (McGrath et al. 2003b).

Barbin et al. (1998) documented eels occupying a variety of depths in the Penobscot Estuary, Maine. The researchers found that American eel moved freely between surface waters and the bottom, and that when movement occurred, it was near the surface on ebbing tides (Barbin et al. 1998).

Upon entering the ocean, American eel appear to migrate in the upper water column. Evidence for this includes physiological changes, including the color change, changes to the visual system, and morphological changes to the swim bladder (McCleave and Kleckner 1985). The color change from yellow to silver provides the American eel with a more countershaded appearance. This form of camouflage is thought to only be effective in the photic zone of the ocean, possibly only in the upper 600 m (McCleave and Kleckner 1985). Other fishes found below 600 m are often dark and not countershaded (Marshall 1971, 1972).

American eel also undergo changes in vision, including an increased eye diameter, an increase in retinal surface area, the addition of new rod cells, an increase of convergence of rods on each neural pathway, decreases in cone density, and changes in vision pigments (Winn et al. 1975; Beatty 1975; Pankhurst 1982; Pankhurst and Lythgoe 1982, 1983). These changes allow the American eel to adapt to the low light conditions they would likely be migrating through (Jerlov 1976; McCleave and Kleckner 1985). Lastly, the swim bladder changes during metamorphosis, allowing American eel to maintain an inflated swim bladder at greater depths (Kleckner 1980).

Tesch (1978a, 1978b) tracked European silver eels (*Anguilla anguilla*) over the European continental slope and found that they swam at depths between 50 and 400 m; the maximum depth in this area was 2000 m. However, the tracking was terminated prematurely due to pressure-transmitter failure. Additionally, Wenner (1973) documented American eel at depths ranging from 15 to 68 m in the Chesapeake Bay, Maryland, and Cape Cod, Massachusetts. The deepest known record for *Anguilla* was reported by Robins et al. (1979) as approximately 2000 m.

Silver eel temperature associations

Temperature may be an important trigger for migrating silver eels, which travel during the fall and winter months. Vøllestad et al. (1986) documented that migrating European eel in Norwegian streams showed the most activity in a temperature range of 9ºC to 18ºC. Similarly, Barbin et al. (1998) documented American eel migrating in September and October in the Penobscot Estuary, Maine, in water temperatures ranging from 9.6ºC to 17.6ºC. Moreover, commercial fishermen in the Elbe estuary have noted that lingering summer temperatures into the fall cause a delay in migration (Tesch 2003).

Like juveniles, mature silver eels utilize a broad range of habitats, and thus are likely to tolerate a wide range of temperatures (Facey and Van den Avyle 1987). A few studies have been done to determine the preferred temperatures of American eel. Barila and Stauffer (1980) reported a temperature preference of 16.7°C, while Karlsson et al. (1984) found that American eel preferred a temperature of 17.4 ± 2.0°C. Haro (1991) reported preferred temperatures of 19.6°C for unmatured silver eels in freshwater, and 15.8 to 18.9 °C for unmatured silver eels acclimated to saltwater.

Silver eel feeding behavior

Silver phase American eel presumably do not feed during their migration to the Sargasso Sea (Gray and Andrews 1971).

Silver eel competition and predation

American eel are preyed upon by many different species, including fish, aquatic mammals, birds, and mammals (mink) (Sinha and Jones 1967; Seymour 1974). However, the importance of American eel as a food source for other animals has not been well recorded in the literature (ASMFC 2000). Thompson et al. (2005) documented the American bald eagle using American eel as a food source. In the Hudson River, New York, 50% of the bald eagle's diet was comprised of 3 fish species, one of which was the American eel (Thompson et al. 2005).

Section II. Identification and Distribution of Habitat Areas of Particular Concern for American Eel

Habitat types that qualify as Habitat Areas of Particular Concern (HAPCs) for American eel include the spawning and hatching grounds, nursery and juvenile habitat, and adult habitat.

Oceanic waters of the Sargasso Sea comprise the spawning and hatching grounds for American eel. This is the only suspected location of reproduction for American eel, and therefore, is essential to the survival of the species. Little is known about American eel habitat in the Sargasso Sea, and the exact location of spawning and hatching has not been identified.

Continental Shelf waters usher the final stage of the larval American eel migration into coastal waters, and are important to larval feeding and growth. This is also where American eel metamorphose into the glass eel stage. Silver-phase eels also cross the shelf during their migration to the Sargasso Sea.

Estuaries and freshwater habitat, including rivers, streams, and lakes, serve as juvenile, sub-adult, and adult migration corridors, as well as feeding and growth areas for juveniles and sub-adults (ASMFC 2000). After American eel larvae transform into glass eels over the continental shelf, they enter estuaries, and ascend the tidal portions of rivers. Glass eels metamorphose into the elver life stage and either continue upstream movements, or cease migrating in the lower saline portions of estuaries and rivers. These estuaries and freshwater habitats serve as foraging grounds for American eel and are important for growth and maturation. American eel can remain in these systems for up to thirty years before maturing and returning to sea.

While estuarine and riverine habitats have been identified as important for the rearing and growth of American eel, many studies failed to find specific American eel habitat associations within them (Huish and Pardue 1978; Meffe and Sheldon 1988; Smogor et al. 1995; Bain et al. 1988; Wiley et al. 2004). Huish and Pardue (1978) found no difference in American eel abundance in relation to width, substrate, flow, and depth in North Carolina streams. Likewise, Bain et al. (1988) found that American eel habitat use was not related to specific habitat features including depth, water velocity, and substrate in two Connecticut River tributaries. Wiley et al. (2004) also did not find any eel-stream habitat relations. The researchers found that eel density was correlated with distance from the ocean (Wiley et al. 2004). While anguillid eels have the ability to survive in a wide variety of habitats, water quality is still an important factor to their health and survival.

Given the great variation in demographics that occurs across latitudinal and distance-inland gradients, all areas may not contribute equally to American eel production and recruitment. Despite this, geographic patterns of differential recruitment are unexplored. This issue must be addressed before identifying specific Habitat Areas of Particular Concern.

Section III. Present Conditions of Habitat and Habitat Areas of Particular Concern for American Eel

Habitat quantity

Much of American eel habitat has not been quantified. American eel utilize a wide range of habitat types throughout their life history, including the Sargasso Sea, oceanic waters off the continental shelf, estuaries, and rivers. Some researchers think that habitat availability for American eel growth areas is rapidly declining. An extreme example by Busch et al. (1998) showed that stream habitat for American eel was reduced from 556,801 km to 90,755 km by dams (assuming that all dams completely block all migration). According to Busch et al. (1998), 15,115 dams block upstream and downstream migrations. Fortunately, American eel are habitat generalists, and therefore may be somewhat resilient to impacts on habitat availability. The increased human impact on aquatic habitat in recent years may not have had as high an impact on American eel as on other diadromous species because they are able to survive and thrive under a variety of conditions.

In general, the use of the estuarine and marine habitat by American eel is less well known than freshwater habitat utilization. Consequently, little information is known on requirements for mature, egg, and larval stages of this species. This is important to note because the marine and estuarine portions of the total population could be quite significant.

Habitat quality

The quality of American eel habitat has been impacted by human actions. Since European settlement, habitat loss has potentially contributed to a possible decline in stocks. However, anthropogenic impacts on American eel at the population level are poorly understood and the magnitude of these threats remains unknown.

Section IV. Significant Environmental, Temporal, and Spatial Factors Affecting Distribution of American Eel

Table 7-2. Significant environmental, temporal, and spatial factors affecting distribution of American eel. This table summarizes the current literature on American eel habitat associations. For most categories, optimal and tolerable ranges have not been identified, and the summarized habitat parameters are listed under the category reported. In some cases, unsuitable habitat parameters are defined. NIF = No Information Found. N/A = Not Applicable. Reported = Ranges or information recorded in the literature.

Life Stage	Time of Year and Location	Depth (m)	Temperature (^{o}C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Silver eel (spawning)	From February to April in Sargasso Sea; spawn in thermal fronts that separate southern and northern water masses; 19.2°N to 29°N and 52°W to 79°W	**Tolerable:** NIF **Optimal:** NIF **Reported:** Upper few hundred meters of the water column	**Tolerable:** NIF **Optimal:** NIF **Reported:** 18-19	**Tolerable:** NIF **Optimal:** NIF **Reported:** Maximum 36.6	**Tolerable:** N/A **Optimal:** N/A **Reported:** N/A	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF
Egg	Same as spawning	**Tolerable:** NIF **Optimal:** NIF **Reported:** Assumed that hatching occurs in the water column	**Tolerable:** NIF **Optimal:** NIF **Reported:** Hatching occurs at 23 in Japanese eel	**Tolerable:** NIF **Optimal:** NIF **Reported:** Sea water	**Tolerable:** N/A **Optimal:** N/A **Reported:** N/A	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF
Leptocephali (larval)	Larvae drift and swim in upper water column for a couple of months; distributed by water currents (e.g., Antilles, Florida, and Gulf Stream); transform into glass eels over continental shelf	**Tolerable:** NIF **Optimal:** NIF **Reported:** Found in upper 250; vertical migrations occur 50-300	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF	**Tolerable:** NIF **Optimal:** NIF **Reported:** Sea water	**Tolerable:** N/A **Optimal:** N/A **Reported:** N/A	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF

Life Stage	Time of Year and Location	Depth (m)	Temperature (^{o}C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Glass eel/elver	Migrations from late winter to early spring (earlier in South than North) into estuaries, and ascend rivers along Atlantic coast	**Tolerable:** NIF **Optimal:** NIF **Reported:** Variety	**Tolerable:** NIF **Optimal:** NIF **Reported:** 10-12 triggers migrations; utilize wide range of temperatures	**Tolerable:** NIF **Optimal:** NIF **Reported:** 0 – 25	**Tolerable:** NIF **Optimal:** NIF **Reported:** Burrow during the day and in between movements upstream in sand, mud, tubes, snags, plant masses, and other materials	**Tolerable:** >25 $cm{\cdot}s^{-1}$ **Optimal:** NIF **Reported:** Upper limit is 35 $cm{\cdot}s^{-1}$: Most will not swim in waters > 25 $cm{\cdot}s^{-1}$	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF
Yellow eel	May continue migrating upstream (March through October; peak May/June) and eventually settle into any habitat available (e.g., estuaries, lakes, ponds, rivers, and streams) for up to 30 years	**Tolerable:** NIF **Optimal:** NIF **Reported:** Variable depending on system	**Tolerable:** Variable **Optimal:** NIF **Reported:** Migration thought to be linked to temperature; increases in migration occur >20	**Tolerable:** NIF **Optimal:** NIF **Reported:** Variety; high tolerance for changes in salinity	**Tolerable:** NIF **Optimal:** NIF **Reported:** Bottom/substrate oriented; most prefer coarse substrates	**Tolerable:** NIF **Optimal:** NIF **Reported:** Highest density in areas with a large variety of velocities and depths	**Tolerable:** NIF **Optimal:** NIF **Reported:** >4
Silver eel (migratory)	Migrate out to sea after maturation; migrations begin at different times depending on location, but occur mostly during the fall, although winter and summer migrations have been documented	**Tolerable:** NIF **Optimal:** NIF **Reported:** Depths vary and may be related to light intensity and turbidity	**Tolerable:** NIF **Optimal:** 17.4±20; activity decreases around 12 **Reported:** Tolerate wide range of temperatures	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF	**Tolerable:** N/A **Optimal:** N/A **Reported:** NIF	**Tolerable:** NIF **Optimal:** NIF **Reported:** N/A	**Tolerable:** NIF **Optimal:** NIF **Reported:** NIF

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