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SPECIES PROFILES: LIFE HISTORIES AND ENVIRONMENTAL
REQUIREMENTS OF COASTAL (U) GEORGIA COOPERATIVE FISHERY
RESEARCH UNIT ATHENS M J AVYLE JUL 84 WES/TR/EL-82-4

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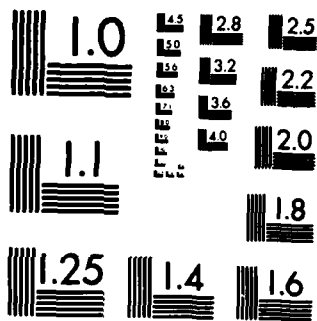
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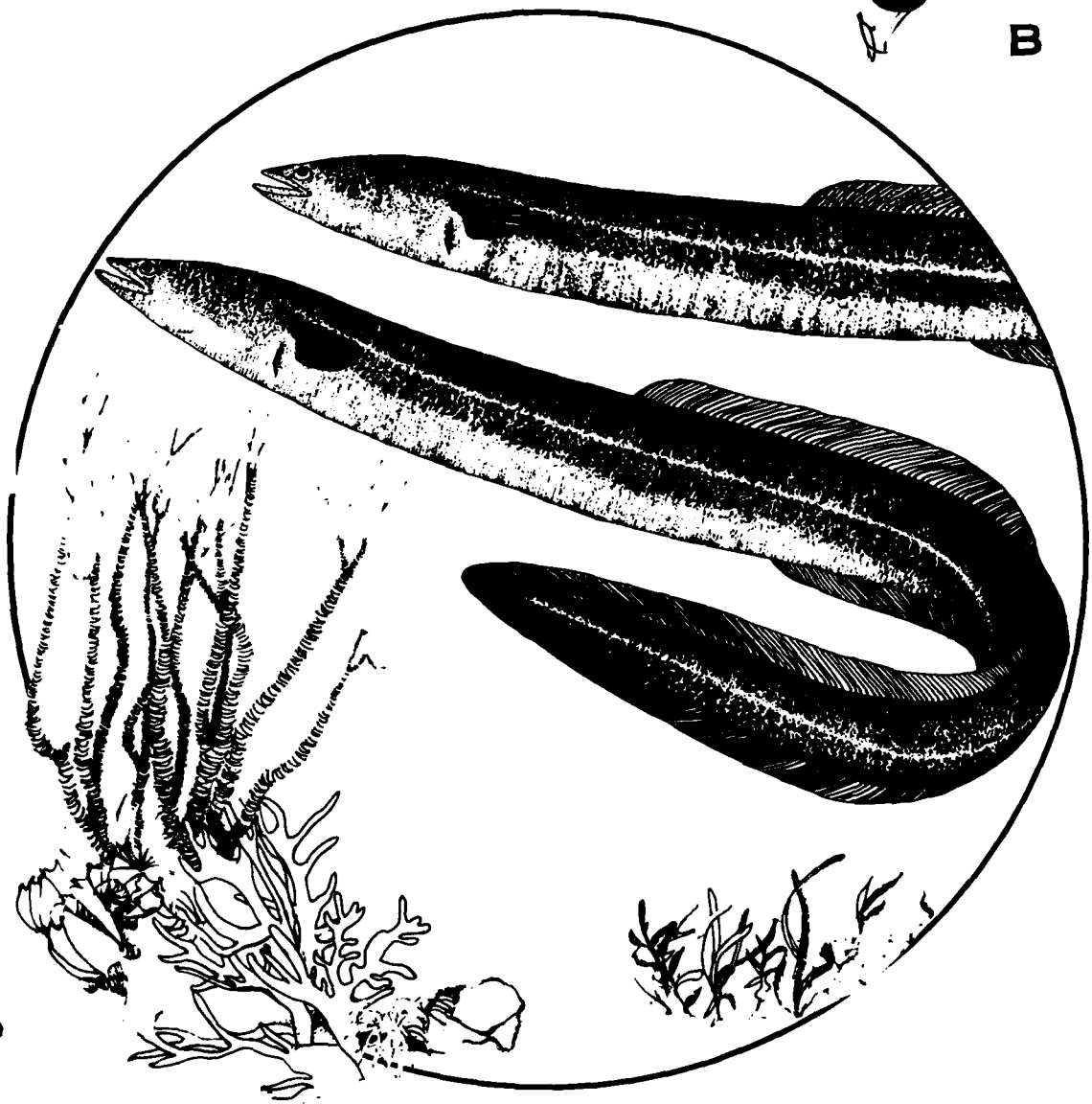
**Species Profiles: Life Histories and
Environmental Requirements of Coastal Fishes
and Invertebrates (South Atlantic)**

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Species Profiles: Life Histories and Environmental
Requirements of Coastal Fishes and Invertebrates (South Atlantic)

AMERICAN EEL

by

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This study was performed for
Coastal Ecology Group
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and

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

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CONVERSION FACTORS

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
acres	0.4047	hectares
square miles (mi ²)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal unit (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

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Dr. Gene Helfman, Earl Bozeman, and Doug Facey, University of Georgia, and Dr. Arnold G. Eversole, Clemson University, reviewed earlier drafts of this Species Profile and provided current information that otherwise could not have been included.

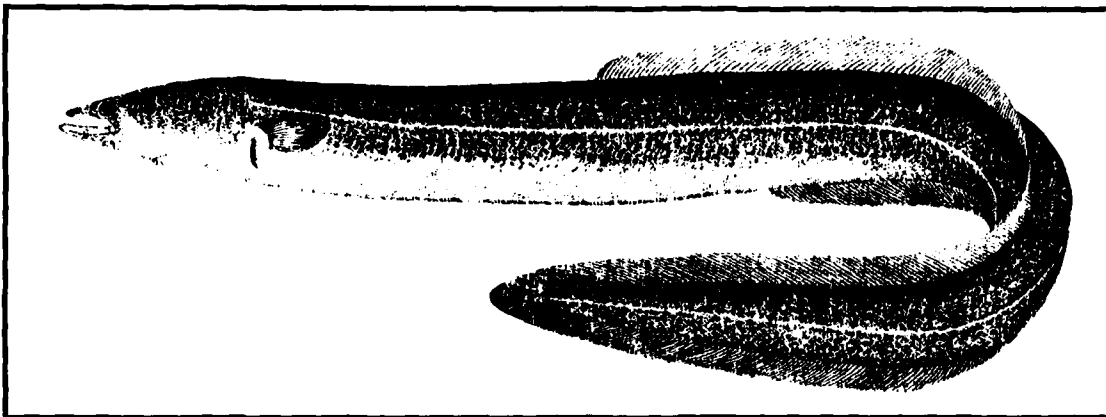


Figure 1. American eel.

AMERICAN EEL

NOMENCLATURE/TAXONOMY/RANGE

Scientific name . . . Anguilla rostrata
 Preferred common name . . . American
 eel (Figure 1)
 Other common names Anguille,
 yellow eel, green eel, black eel,
 little eel, bronze eel, glass
 eel, silver eel, river eel
 Class Osteichthyes
 Order Anguilliformes
 Family Anguillidae

Geographic range: Adults or various developmental stages occur in freshwater rivers, coastal waters, and the open ocean from the southern tip of Greenland, Labrador, and Newfoundland southward along the Atlantic coast of North America, into the Gulf of Mexico as far as Tampico, Mexico, and in Panama, the Greater and Lesser Antilles, and southward to the northern portion of the east coast of South America (Tesch 1977). The species is abundant from Maine to Mexico, is resident

in the Mississippi Valley, and occurs in the West Indies and Bermuda (Figure 2). Bertin (1956) reported the latitudinal range for the American eel as 5° to 62° N. It occurs in warm brackish and freshwater streams, estuaries, and coastal rivers. The American eel sometimes occurs in cold freshwater trout streams in mountainous regions. Adults are occasionally found in landlocked lakes, primarily in the Northeastern United States. Its distribution has increased because of its hardiness and the ease with which it can be transplanted into new habitats.

MORPHOLOGY/IDENTIFICATION AIDS

American eels undergo a series of morphological changes in their life cycle; these characteristics are presented in the LIFE HISTORY section. The following material was summarized primarily from Fahay (1978) and Tesch (1977).

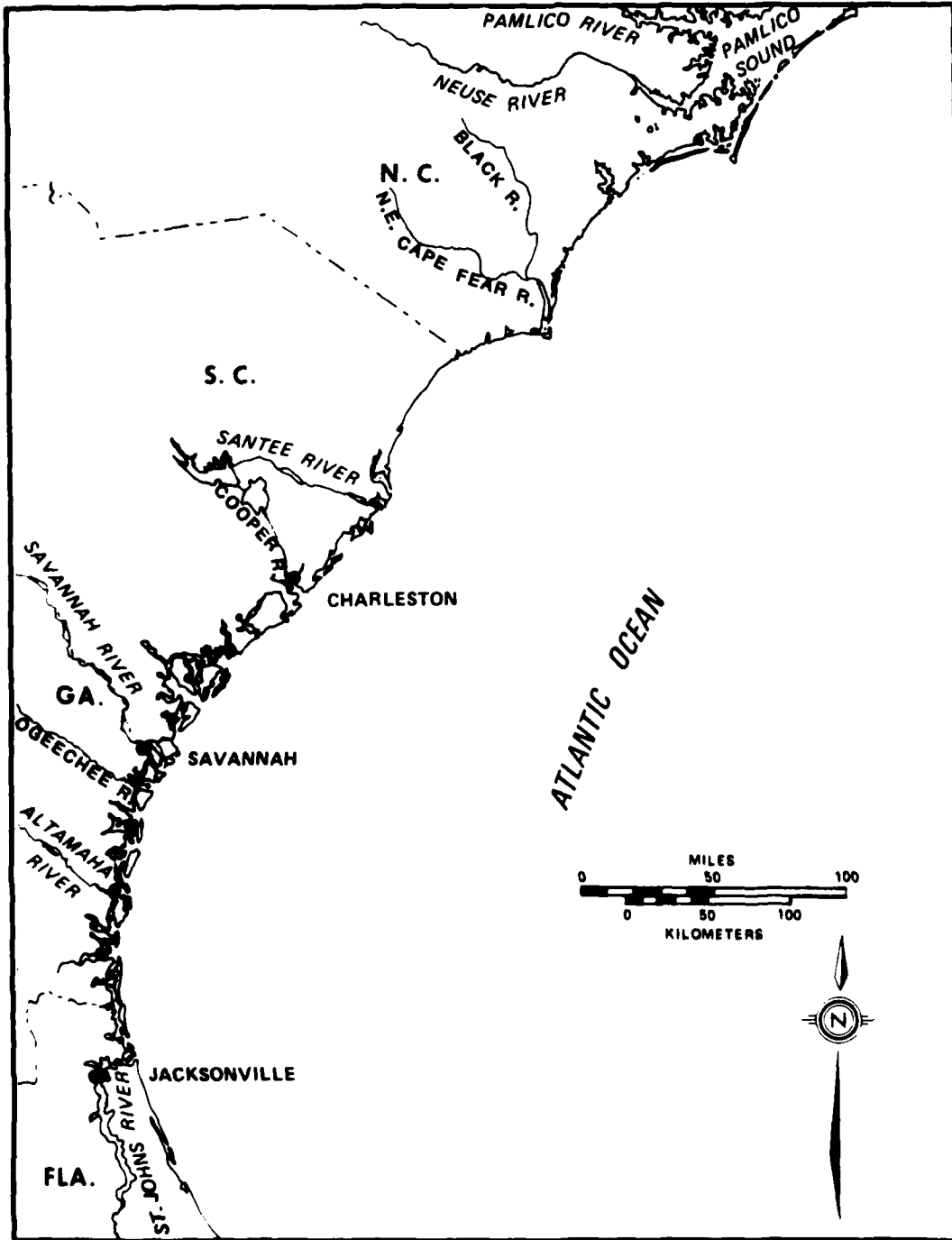


Figure 2. Major rivers that support the American eel in the South Atlantic Bight. Eels also are common in other freshwater tributaries, and in bays and estuaries.

The body is elongate and snake-like (Figure 1). The dorsal and anal fins are confluent with the rudimentary caudal fin. Pectoral fins are present, but ventral (pelvic) fins are absent. The body is covered by minute embedded scales (often causing specimens greater than 3 to 5 years of age to appear scaleless). The lateral line is well developed. The mouth is terminal; jaws contain bands of small, pectinate or setiform teeth. A long tooth patch also occurs on the vomer. The number of vertebrae ranges from 103 to 111 but usually is 106 to 108 (Schmidt 1913).

No other anguillid eels occur in North American coastal waters, but the American eel's spawning grounds coincide closely with those of the European eel (*Anguilla anguilla*). Externally visible traits of the two specimens are similar; however, the European eel has 111-119 vertebrae (mean = 115). Ege (1939) presented comprehensive morphological data for *A. rostrata*. Some authors have argued that European and American eels should be regarded as geographical variants of the same species, but this is not generally accepted at present (Fahay 1978).

No data are available that conclusively point to geographic variations in morphology, and no subpopulations have been distinguished. Koehn and Williams (1978) noted protein differences among juvenile eels collected from different locations along the Atlantic seaboard, but they concluded that the differences were due to variations in selective pressures among environments in which growth occurred.

REASON FOR INCLUSION IN SERIES

The American eel supports valuable commercial and limited recreational fisheries throughout most of its range. Harvested adults often are shipped alive or frozen to Europe where they frequently are smoked

before marketing, and a fishery for elvers (immature eels typically less than 60 mm long) has recently begun in the South Atlantic Bight. Elvers are shipped to Japan where they are cultured in ponds. Pond rearing of eels in the United States is in a developmental stage, and there is a potential for development and expansion of an eel culture industry.

The American eel is an important prey species of larger marine and freshwater fishes and is a predator on a variety of other animals including commercially important crabs and clams. Eels contribute to the loss of nutrients from freshwater rivers and lakes because of their great organic intake, large numbers, lengthy stay in freshwater, and subsequent migration to sea (Barila and Stauffer 1980). Alteration of river flow into estuaries could affect upstream migration of immature eels.

LIFE HISTORY

The life cycle of the American eel includes oceanic, estuarine, and riverine phases (Figure 3). Many details of its life history are only generally understood or have been inferred from knowledge of the congeneric European eel. Little has been reported on eel life history in rivers along the South Atlantic Bight; much of the information presented below is based on work in Middle and North Atlantic areas of the United States and Canada.

Different stages of the eel's life cycle are known by a variety of common names that are used throughout the scientific literature. The larvae are called leptocephali (sing. = leptocephalus); they first metamorphose into unpigmented "glass eels" that gradually develop pigmentation and are then called elvers. Elvers migrate into freshwater where they remain several (sometimes many) years and are called yellow eels. Yellow

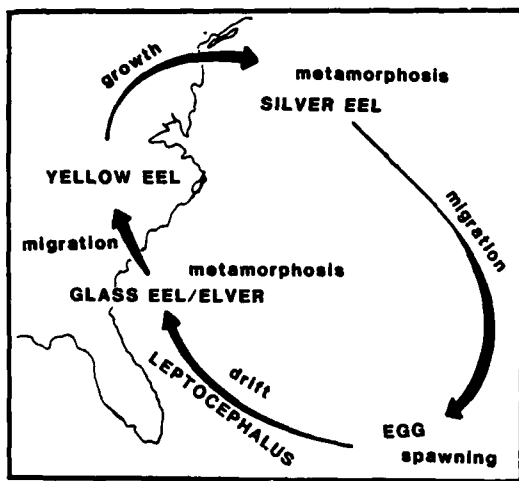


Figure 3. Diagrammatic representation of the American eel's life history.

eels may be sexually undifferentiated (gonads contain no definable gametes), hermaphroditic (oogonia and spermatogonia present), or sexually differentiated (females with oogonia; males with spermatogonia present), but none of these stages are capable of reproduction and, hence, all yellow eels are immature. Maturation is accompanied by changes in body color and morphology; maturing eels migrate downriver and through the ocean to the spawning grounds and are known as "bronze eels" or "silver eels." Details of life history for these stages are provided below.

Spawning

The American eel is catadromous. It spawns in the sea but spends most of its life in rivers, freshwater lakes, and sometimes estuaries. After maturity it returns to the sea (Figure 3). The age at maturity has not been well defined; Fahay (1978) reported that maturation occurred beyond age III for males and at age IV-VII for females from northerly populations, but recent data suggest that maturation is more rapid in populations along the South Atlantic Bight.

Helfman and Bozeman (unpublished MS.¹) collected sexually differentiated males and females at age III² in the Altamaha River, Georgia, and concluded that females there may have matured at earlier ages and smaller sizes than eels in northern areas whereas males matured at the same age and size as northern eels. Hansen and Eversole (in press) and Harrell and Loyacano (1980) collected differentiated males and females as young as age II and III, respectively, in the Cooper River, South Carolina.

Prior to seaward migration in the fall, maturing eels begin a metamorphosis into the silver eel stage, as described in the Yellow and Silver Eels section.

Eels migrating from Chesapeake Bay are in a more advanced state of metamorphosis than those migrating from Canadian waters; this supposedly enables eels to reach the southern spawning grounds in relatively short stages of maturity (Wenner and Muck 1974). The difference in the extent of metamorphosis between migrating eels from Canada and Chesapeake Bay suggests that migrating eels in South Atlantic rivers could be even further developed than those in Chesapeake Bay at the outset of migrations. Helfman and Bozeman (unpublished MS.¹) concluded that reproductive migrations from the Altamaha River, Georgia, occurred during late winter or early spring, but Hansen and Eversole (in press) and Michener (1980) indicated that migrations occurred during the fall in the Cooper River, South Carolina.

¹Population attributes of American eels in a Georgia river. G. S. Helfman and E. L. Bozeman, Department of Zoology and Institute of Ecology, University of Georgia, Athens, GA 30602. Submitted to Trans. Am. Fish. Soc.

²In this case, age is the number of years spent in freshwater (see the GROWTH CHARACTERISTICS section for aging methods).

Few details are known about the oceanic spawning migration of the American eel. The first collections of adults in offshore waters were reported by Wenner (1973) in the open ocean southeast of Cape Cod, Massachusetts, east of Assateague Island, North Carolina, and southeast of Chesapeake Bay. The means by which eels navigate to spawning grounds are poorly understood. Miles (1968) concluded that the eel was capable of noncelestial orientation (southward), and Rommel and Stasko (1973) indicated that eels may use geoelectric fields generated by ocean currents to navigate. Robins et al. (1979) photographed two adult *Anguilla* eels on the floor of the Atlantic Ocean in the Bahamas at depths of about 2000 m, and although it was impossible to determine if the specimens were European or American eels, the authors believed them to be prespawning *A. rostrata*.

Stasko and Rommel (1977) tracked five migrating eels in the lower St. Croix River Estuary, New Brunswick, Canada, and found that one eel moved 25 km in 20 hr and another moved 38 km in 40 hr. Eels they studied showed considerable vertical movements in the water column; behavior did not change with diel or tidal cycles. Silver European eels traveled at 44 km per day when migrating to spawn (Tesch 1977). Edel (1976) believed that the depth at which American eels migrate in the ocean varied with light intensity so that swimming depth would vary with turbidity of the water.

Spawning by American eels has never been directly observed, and spawning areas have been delineated on the basis of collections of larvae. Spawning apparently occurs in the Sargasso Sea as early as January or February and may continue into August. Tesch (1977) summarized work by Schmidt (1923), Vladykov (1964), Smith (1968), and Vladykov and March (1975), and showed a spawning zone south of Bermuda and north of the Bahamas that is centered at about 25° N and 69° W.

The youngest stages of American eel larvae coexist with European eel larvae, but American eel larvae predominate west of 62° W and south of 24° N (Fahay 1978). Fahay also reported that *A. rostrata* larvae have not been found east of 50° W.

The depth at which spawning occurs is not known, but Taning (1938) reported that larvae collected near Bermuda occurred only at depths between 550 and 2200 m. Egg diameter of *A. rostrata* is about 1.1 mm (Tesch 1977). Incubation periods of American eel eggs are not known.

Fecundity is 10 to 20 million eggs per female (Vladykov 1955, cited by Fahay 1978; Eales 1968). Relationships between eel size and fecundity for 21 eels were reported by Wenner and Musick (1974) as:

$$\log F = -4.29514 + 3.74418 \log TL, \text{ or} \\ \log F = 3.2290 + 1.1157 \log W;$$

Where F = number of eggs per female,
TL = total length, mm, and
W = total weight, g.

Adult eels presumably die after spawning. None have been observed to migrate up rivers, and occurrences of spent eels have not been reported.

Larval (Leptocephalus) Stage

Hatching occurs from February through August (Vladykov and March 1975; Fahay 1978), and the larval stage lasts about 1 year or perhaps longer. The body is lanceolate in shape, sharply pointed at both ends, and deepest at the middle (see Tesch [1977] or Fahay [1978] for illustrations). The size at hatching has not been described, but Schmidt (1925) collected 7- to 8-mm larvae in February. The smallest larvae collected by Vladykov and March (1975) and Smith (1968) were 12 mm and 17 mm, respectively.

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Work done by Hinton and Eversole (1978, 1979, 1980) on toxicity of aquaculture chemicals to various life stages of eels suggests that tolerance to chemicals increases with size or age.

Environmental Factors and Sex Determination

There is limited evidence which suggests that the gender of American eels is determined to some extent by environmental factors. Fahay (1978) stated that the sex of the European eel can be environmentally influenced, but indicated that the factors responsible could only be speculated upon. The long developmental period in fresh- or brackish waters in combination with juvenile hermaphroditism (see the LIFE HISTORY section) provides a setting in which environmental factors could regulate the gender of eels.

Female American eels predominate in upstream freshwater areas as well as in northerly stocks, but there is no direct evidence of mechanisms that lead to these patterns. One possible explanation is that male leptocephali and elvers do not migrate as far as females (and hence remain in southerly or downstream areas [Fahay 1978]). But because eels do not mature until they have lived 3 yr (males) to 7 yr (females) or longer in freshwater, it is unlikely that physiological systems capable of causing sex-related differences in migratory patterns would be

developed in the youngest life stages. It is possible that male eels prefer higher salinities than females and move downstream to coastal areas after they are differentiated, but this behavioral pattern has not been observed and it would not explain the latitudinal trend.

Koehn and Williams (1978) reported that eels throughout the species' range are part of the same spawning stock. They concluded that differences in protein characteristics in yellow eels from different drainages along the Atlantic coast reflected environmental differences. This suggests that latitudinal variations in the sex ratio are not genetically determined but could be due to variations of environmental factors. Some of the environmental factors that could be involved include food quality and population density (Fahay 1978). Parsons et al. (1977) believed that stocking of European eel elvers into Lough Neagh, Northern Ireland, led to a higher population density and a marked increase in the proportion of male eels that subsequently emigrated from the lake. Similarly, Egusa (1979) indicated that A. anguilla elvers grown in Japanese ponds under crowded conditions produced males predominantly, suggesting that variations in the sex ratio of American eel populations may be related to population density. Salinity apparently is not an important sex determinant; sex ratios were similar in the freshwater and brackish culture ponds studied by Egusa.

fact that the species occurs throughout a gradient of strictly fresh to brackish waters. Leptocephali are in near-ionic equilibrium with sea water (Hulet et al. 1972).

Dissolved Oxygen

Dissolved oxygen requirements have not been thoroughly documented, but eels generally will select water with high oxygen tension (Hill 1969). Commercial shipping of live eels indicates that they are especially hardy. Elvers can be packed densely and shipped alive by being dampened but not covered with water because they can absorb 60% of required oxygen through their skin (Sheldon 1974, cited by Fahay 1978). Tesch (1977) stated:

"The capacity of the adult eel to survive in both air and water is associated with its ability to use both branchial and cutaneous modes of respiratory gas exchange. The eel survives better in air than in poorly oxygenated or polluted water"

Habitat Structure

Postlarval eels tend to be bottom dwellers and hide in burrows, tubes, snags, plant masses, other types of shelter, or the substrate itself (Fahay 1978). This behavior is reflected in their food habits, protects them from predators, and influences commercial fishing techniques. Few other freshwater fishes display similar habitat use; therefore, interspecific competition for living space may be limited. The presence of soft, undisturbed bottom sediments is important to migrating elvers as shelter (see the Elver Stage section). EdeI (1979) indicated that eels in his experimental systems were less active when shelter was present than when it was absent. Vladykov (1955, cited by Fahay 1978) reported that adult eels in northern habitats lie dormant in the bottom mud during winter.

Ford and Mercer (1979) used mark-recapture methods to obtain a population estimate of 350 yellow eels in a 600-m section of a marsh creek in a Massachusetts estuary. They studied the behavior of yellow eels and found that eels shorter than 30 cm predominated in narrow, soft-bottomed, upper marsh creeks whereas those longer than 30 cm predominated in wider, lower marsh creeks having mud and sand bottoms. Most eels had relatively small home ranges and rarely moved more than 100 m from the point at which they were initially caught. The authors believed that large eels may establish territories in lower marsh areas and thereby restrict smaller eels to smaller high marsh creeks.

River and Tidal Currents

The elver's nocturnal activity patterns and reliance on tides and river currents for upstream movement are presented in the LIFE HISTORY section.

Movements of yellow eels in a tidal creek in Georgia were affected by tides and time of day (Helfman et al. 1983). Daytime movements of eight telemetered eels were restricted to the main creek channel, but at night the fish were near the mouths of feeder creeks at low tide or in flooded marsh areas during high tide. Helfman et al. (1983) termed this movement "a nocturnal activity pattern modified by tidal flow." They suggested that movements onto the marsh at night may have been foraging trips.

Contaminants

Little work has been done on American eels regarding toxic effects of pollutants or tolerance limits. Tolerance would be expected to vary with developmental phase, and the eel's long residence in freshwater rivers could lead to repeated doses of toxicants and accumulation to toxic levels (Holmberg and Saunders 1979).

fish eaten were bottom dwellers, reflecting the eels' tendency to remain near the bottom. Fahay (1978) concluded that eels depend more on scent than sight to obtain food.

Little has been published about predation on eels. Hornberger et al. (1978) reported that elvers and small yellow eels were eaten by largemouth bass (Micropterus salmoides) and striped bass (Morone saxatilis) in the Cooper River, South Carolina, but eels never were a major component of these predators' diets. Leptocephali, glass eels, elvers, and small yellow eels probably are consumed by a variety of other predatory fishes; grown eels are eaten by other species of eels and by gulls, bald eagles, and other fish-eating birds (Sinha and Jones 1967; Seymour 1974).

Crane and Eversole (1980) found no parasites on glass eels migrating into the Cooper River, South Carolina, but four genera of protozoans (Trichodina, Ichthyophthirius, Myxidium, and Myxobolus) and one species of monogenetic trematode (Gyrodactylus anguillae) were found on elvers. Crane and Eversole (in press) reported that 214 of 218 yellow eels collected from brackish waters of the Cooper River, South Carolina, were parasitized by one or more of 22 helminth species. Parasites of American eels in Quebec included protozoans, trematodes, nematodes, cestodes, and copepods (Hanek and Molnar 1974). The myxosporidian protozoan, Myxidium zelandicum, has been found in the kidneys and on the gills of A. rostrata (Komourdjian et al. 1977).

ENVIRONMENTAL REQUIREMENTS

Temperature

The eel's broad geographic range and diverse habitats suggest flexible temperature requirements. Elvers and yellow eels live in waters ranging from cold, high-elevation or high-

latitude freshwater streams and lakes to warm, brackish coastal bays and estuaries in the Gulf of Mexico. Jeffries (1960) found elvers at temperatures as low as -0.8°C .

Barila and Stauffer (1980) acclimated yellow eels to a range of temperatures between 6°C and 30°C and then measured preferred temperatures. Although preferred temperatures tended to increase with increased acclimation temperature, differences among groups were nonsignificant, and the authors reported a final temperature preference of 16.7°C . They also reported that feeding ceased at temperatures below 14°C . Marcy (1973) reported that American eels survived passage through the cooling system of a nuclear power plant, during which they were exposed to elevated temperatures for 1-1.5 hr. Poluhowich (1972) suggested that the American eel's multiple types of hemoglobins serve to maintain a relatively constant blood oxygen affinity when the eel is exposed to temperature changes.

Salinity

The mechanisms by which glass eels or elvers orient during their shoreward migration have not been described, but their movements probably are keyed to salinity gradients after they reach coastal waters. European glass eels and elvers become positively rheotactic when they first encounter freshwater that is mixed with seawater (Tesch 1977); thus salinity as well as the current itself may provide the gradient for shoreward orientation. Alterations of patterns or magnitudes of freshwater inflows to bays or estuaries could alter salinity regimes and thereby affect the number, timing, and spatial patterns of upstream migrations by elvers.

As with temperature, salinity requirements of postlarval eels can be generally inferred as "broad" from the

The feasibility of commercial grow-out operations in North Carolina was assessed by Easley and Freund (1977). Interest in culturing was stimulated by rising prices noted above during the late 1960's and early 1970's, but considerable refinement of techniques is needed. Development of eel aquaculture has focused on methods for collecting elvers and on physical features of grow-out systems. Hormone injections can be used to induce maturation of female American eels (Edel 1976), but proper spawning conditions are unknown, and eel culture remains dependent on capturing wild elvers. Hinton and Eversole (1978, 1979, 1980) evaluated the toxic effects of chemicals commonly used in aquaculture to glass eels (mean length of 55 mm), elvers (mean length of 97 mm), and yellow eels collected from South Carolina rivers.

The South Atlantic States have few, if any, restrictions specifically designed to regulate yellow or silver eel harvest, but fisheries for yellow eels often have been nonexistent or minimal because of prohibitions against using traps in freshwaters (as mentioned above for Georgia). Such restrictions generally are intended to prevent incidental catches of sport fishes. Mouth diameter and wire mesh sizes of traps are regulated in some areas to reduce catches of other species (e.g., Hornberger et al. 1978). Elver fishing is illegal in Georgia.

Estimates of density, mortality, or other vital statistics of eel stocks generally have not been reported, and factors regulating survival or stock size have not been evaluated. Helfman (unpublished MS.) suggested that the eel's long life in freshwaters may make the stocks prone to local overharvest. Keefe (1982) suggested that recent declines in catch per unit effort of eels in North Carolina indicated overharvest. Because all American eels spawn in the Sargasso Sea and there apparently are

no genetically distinct stocks or subpopulations (Koehn and Williams 1978), overharvest in one region could affect recruitment in other regions. Nevertheless, some management policies allow or encourage local heavy exploitation of migrating silver eels or elvers under the assumption that the numbers of elvers returning in later years will be maintained by escapement of spawning stock from other areas.

No major sport fishery for American eels exists in coastal rivers of the South Atlantic Bight, but the species is caught incidentally by anglers in estuaries and rivers.

ECOLOGICAL ROLE

Yellow eels are nocturnal and a significant portion of their feeding occurs at night. The diet is diverse and generally includes nearly all types of aquatic fauna that occupy the same habitats. Eels swallow some types of prey whole, but they also can tear pieces away from larger dead fish, crabs, or other items. Eels in freshwater feed on insects, worms, crayfish and other crustaceans, frogs, and fish whereas elvers in saltwater are planktivorous. Elvers collected from the Cooper River, South Carolina, consumed aquatic insects (mainly chironomid larvae and adults), cladocerans, amphipods, and fish parts (McCord 1977). The diet of yellow eels from the Cooper River varied with eel size and season. Intermediate size classes contained more types of food than elvers or maturing eels; fish occurred in the diet primarily in winter and spring whereas insects and mollusks were eaten from spring through fall. Crustaceans, bivalves, and polychaetes were the major prey of eels in lower Chesapeake Bay; blue crabs and soft clams were significant prey (Wenner and Musick 1975). Eels shorter than 40 cm in New Jersey streams mainly ate aquatic insects whereas larger eels fed mostly on fish and crustaceans (Ogden 1970). Most

fishermen and secondarily provided bait used in blue crab (Callinectes sapidus) traps. A larger commercial fishery for eels in the region is developing, and glass eels, elvers, yellow eels, and silver eels are exploited. Techniques for capturing and growing elvers to marketable sizes are being developed (Easley and Freund 1977).

The European market has been the major outlet of U.S. yellow and silver eel landings (Fahay 1978). Eels are hardy and can be densely packed and shipped alive if they are kept moist, cool, and supplied with oxygen. Live eels are preferred in Europe, but many are shipped frozen.

Commercial fishermen use a variety of methods, including lift nets, drift nets, traps, weirs, otter trawls, pound nets, fyke nets, spears, handlines, eel pots, haul seines, and gill nets (Fahay 1978). The fyke net is the major gear used in North Carolina to exploit eels that are moving seaward in late summer or early fall to begin their spawning migration. Yellow eels in fresh- or brackish waters are primarily taken with baited traps or eel pots.

Fahay (1978) summarized catch statistics along the Atlantic coast for 1955-73. Landings from the Middle Atlantic (New Jersey-Virginia) consistently exceeded those from the North Atlantic and South Atlantic States, but landings from Southern States increased in the late 1960's and early 1970's. For 1955-64, the South Atlantic harvest averaged about 37,000 kg annually, and for 1965-73, annual landings were about 630,000 kg. The value of these landings ranged from \$8,000 to \$83,000 annually for 1965-73.

Eel harvest and value in North Carolina dramatically increased in the 1960's and 1970's (Easley and Freund 1977). For 1960-70, average annual landings were 17,800 kg valued at

\$0.11/kg; in 1972-73, the price rose to \$0.35/kg; and in 1973-76, landings averaged 151,200 kg at a price of \$0.92/kg. Catch value ranged from \$0.95 to \$1.85/kg and harvest averaged 285,000 kg for 1977-79 (Keefe 1982). The bulk of the North Carolina landings is taken from northeastern coastal areas.

In Georgia, commercial fishing for eels in freshwater was effectively prohibited prior to 1980 because of restrictions against using traps in inland waters. Harvest in 1979 was about 3,900 kg (Helfman, unpublished MS⁴). After a freshwater trap fishery was allowed in 1980, harvest was 50,000 kg, but landings in 1981 and 1982 were 5,500 kg and 16,800 kg, respectively. The 1982 catch was valued at \$35,000 or \$2.08/kg.

A fishery for European eel elvers began in Europe during the late 1960's to supply Japan's demand for young eels to use in pond aquaculture. Experimental work on techniques for capturing migrating American eel elvers has been done in the St. Johns River, Florida (Topp and Raulerson 1973). Elvers were packed live in boxes and shipped to Japan, where prices paid for local Anquilla japonica elvers were \$7/kg in 1965-68, \$300/kg in 1969, and \$330 to \$925/kg in 1971-73 (Fahay 1978; Egusa 1979). Prices paid for European eel elvers in Japan initially were equivalent to those paid for local elvers, but European eels were inferior in the pond culture systems (poor growth and disease problems); in 1973, the Japanese paid only \$30 to \$50/kg for European elvers (Egusa 1979). Accounts of American eel performance in Japanese eel culture were not located.

⁴Development and expansion of the fishery for American eels in Georgia. G.S. Helfman, Department of Zoology, University of Georgia, Athens, GA. 30602. Project summary, University of Georgia Sea Grant Program, 1983.

fifth year of life and the scales formed annual rings in subsequent winters (Smith and Saunders 1955). Thus, in northerly areas, age in years generally will be the number of scale rings plus three. The eel, however, continues to form scales as it grows, leading to a situation in which different scales from the same fish can give different ages (Smith and Saunders 1955).

Growth rates within year classes are highly variable, leading to considerable variation in length at age and poor predictability of age from size. Lengths of eels at various ages in northerly populations are summarized in Table 1. Few growth data for eels in South Atlantic States have been reported. Harrell and Loyacano (1980) reported that eels in the Cooper River grew 45 to 52 mm per year for ages II-XVI. Helfman and Bozeman (unpublished MS.³) tagged yellow eels in a Georgia estuary and used recap-

ture data to estimate growth rates. There was a slow-growth period during November through February when the fish grew an average of 0.025 mm per day. They grew more rapidly during the rest of the year, gaining an average of 0.220 mm per day. These rates produced an average annual length increase of 57 to 63 mm.

Maximum age of yellow eels collected from northern rivers has been reported to be 15 to 20 years (Fahay 1978). Landlocked eels liberated as elvers in Sherman Lake, Michigan, lived 35 to 40 years (Vladykov 1973). Accuracy of estimates of the age at maturity may be affected by problems with aging techniques.

COMMERCIAL AND SPORT FISHERIES

Prior to the 1970's, the eel fishery in the South Atlantic Bight primarily provided live bait to sport

Table 1. Lengths of American eels at various ages.

Age (yr)	Total length (cm) at various locations							
	Bill's Lake New Brunswick ^a	Crecy Lake New Brunswick ^a	Newfoundland ^b	Lake Ontario ^c	New Jersey ^d	Rhode Island ^e	Delaware River ^f	South Carolina ^g
I	---	---	---	---	---	---	12-16	20-31
II	---	---	---	---	---	---	14-25	21-50
III	20-26	20-22	---	12	---	---	18-28	22-59
IV	22-38	21-27	---	17	29-32	27-46	24-32	28-62
V	26-48	25-35	---	22-37	---	---	26-34	32-66
VI	24-51	29-42	---	22-47	41-67	28-51	28-42	31-68
VII	34-56	30-52	---	22-47	36-67	29-58	29-43	42-74
VIII	38-57	32-55	---	22-47	44-70	33-64	35-47	40-69
IX	38-57	34-59	53-62	32-52	37-74	38-62	35-50	44-73
X	49-57	42-56	60-65	37-62	44-86	37-65	40-52	53-67
XI	---	---	58-69	37-62	63-90	46-65	45-54	65-69
XII	---	---	58-72	37-62	67-94	---	43-64	65-74
XIII	---	---	68-76	47-62	68-98	---	---	---
XIV	---	---	72-80	47-67	78-97	---	56-59	83
XV	---	---	79-87	47-62	78-104	---	---	79
XVI	---	---	88	47-62	77-100	---	---	---
XVII	---	---	92	47-72	95-99	---	---	---
XVIII	---	---	93	62-72	---	---	---	---
XIX	---	---	---	87	---	---	---	---

^aSmith and Saunders 1955.

^bGray and Andrews 1971.

^cHurley 1972.

^dOgden 1970.

^eBieder 1971.

^fJohnson 1974.

^gdata combined from Harrell 1977, Hansen 1979, and Michener 1980.

be a result of incorrect sexing, selectivity of sampling gear and the possible exclusion of smaller males, and the assumption that characteristics for the American eel would parallel those of the European eel. The gender of adult eels is not externally apparent, and gonadal tissues should be examined histologically to avoid errors in sex determination (Dolan and Power 1977; Facey and LaBar 1981).

Age at maturity and other aspects of reproduction are described in the Spawning section. Sexual differentiation does not occur until eels reach about 200 mm in length (Fahay 1978). Prior to completion of the differentiation process, some eels possess gonads containing male and female gametes (juvenile hermaphroditism; Tesch 1977), but after gender is established, it does not change (Fahay 1978). Helfman and Bozeman (unpublished MS.) reported that differentiated and undifferentiated yellow eels in the Altamaha River, Georgia, overlapped considerably in size: undifferentiated eels were as large as 363 mm at age VII; differentiated males were as small as 209 mm at age III; differentiated females were as small as 186 mm at age III; and hermaphrodites, which constituted less than 1% of the collections, ranged from 267 to 328 mm at ages IV to V. Hansen and Eversole (in press) reported similar overlap in size and age of differentiated and undifferentiated eels in the Cooper River, South Carolina.

Yellow eels begin to metamorphose into silver eels in the fall prior to seaward migration. The metamorphosis includes: (1) color change (to a metallic, bronze-black sheen; pectoral fins change from yellow-green to black); (2) fattening of the body; (3) thickening of the skin; (4) enlargement of the eyes (macrophthalmia) and changes in visual pigments in the eye in preparation for migrating at dark ocean depths (Vladykov 1973; Beatty 1975); (5) increased length of capil-

laries in the rete in the swim bladder, which also may be an indication of migrating at great depths (Kleckner and Kruger 1981); and (6) degeneration of the digestive tract. Silver (metamorphosed) eels appear to be better adapted to swimming than yellow eels (Holmberg and Saunders 1979). Presumably, ovaries mature fully only after the migrating female reaches saltwater (Fahay 1978).

GROWTH CHARACTERISTICS

Larvae typically reach 40 to 70 mm after 1 year of growth; Hornberger et al. (1978) collected glass eels from the Cooper River, South Carolina, from January through April that averaged 55 mm in length and ranged from 45 to 65 mm (see the Larval Stage section for growth within the first year). The metamorphosis into elvers is accompanied by a decrease in length and weight due to reduction in water content of the body. Elvers grow slowly and reach about 127 mm after the first year in freshwater (Bigelow and Schroeder 1953). Yellow eels typically grow slowly but can achieve weights up to 6.8 kg; females caught from the St. Lawrence River range from 960 to 1270 mm long and 0.9 to 4.5 kg (Fahay 1978). Females typically grow to a larger size than males.

Eels have been aged from otoliths and scales. Otoliths in eels consist of a translucent nucleus (formed at sea) surrounded by broad opaque summer zones and narrow translucent winter zones (Harrell and Loyacano 1980). Harrell and Loyacano (1980) used otoliths to age American eels from the Cooper River in South Carolina. Distinct annuli were present in 410 of 415 otoliths examined; the opaque ring first appeared in May and the translucent zone was first evident in November. The third opaque ring corresponds to the eel's first growing season in freshwater. Eels in Canadian waters formed their first scales at 160 to 200 mm during their third to

"early" arrivals may be the earliest spawned individuals or a segment of the main body of leptocephali that is moved northward more quickly by localized water currents. Alternatively, these elvers may be "late" arrivals produced from leptocephali that did not metamorphose during the previous winter/spring.

Elvers occupy freshwater-saltwater transition areas before ascending rivers. During this period, elvers are active at night and burrow or rest in deep water during the day (Deelder 1958). This nocturnal behavioral pattern causes the elvers to be transported upstream by flood tides that occur at night, and they drift back down during ebb (Fahay 1978). Pacheco and Grant (1973) reported similar patterns for elvers at the mouth of the Indian River, Delaware, and Tesch (1977) noted equivalent behavior by European eel elvers. He also indicated that *A. anguilla* elvers orient to river currents for upstream movement, and if the current becomes too weak or too strong (velocities not specified), eels may move into backwater areas, severely delaying upstream progress. Basic similarities in behavior of European and American eel elvers suggest that *A. rostrata* elvers would be similarly affected by extremely fast or slow river currents.

Fahay (1978) stated that as upstream migration to freshwater streams begins, males tend to stay in brackish water while females move into fresher water, but this is based on observed distribution patterns of older eels rather than direct observation of elver behavior. When elvers cease their migration, they begin a growth and differentiation period in which they are called yellow eels.

Yellow and Silver Eels

Many authors (e.g., Bigelow and Schroeder 1953; Vladykov 1966) have stated that yellow eel females occur

primarily in freshwaters whereas males are generally found in salt- or brackish waters. Dolan and Power (1977), however, concluded that an extensive review of literature did not support this "female-freshwater, male-saltwater" theory. Recent studies continue to be inconsistent. Helfman and Bozeman (unpublished MS³) found that females represented 94% of the sexually differentiated yellow eels collected from freshwater areas of the Altamaha River in Georgia and 64% of the differentiated yellow eels in estuarine areas. However, collections of eels from the Cooper River, South Carolina, showed a minor variation of sex ratio from fresh- to saltwater. Females contributed 97%, 95%, and 93% of the differentiated eels collected from fresh-, brackish-, and saltwater areas, respectively (Harrell and Loyacano 1980; Michener 1980; Hansen and Eversole, in press).

In addition to the freshwater-saltwater variation in the sex ratio, a geographic variation in the distribution of the sexes has been hypothesized. Vladykov (1966) stated that male eels predominate in middle and southern Atlantic populations (New Jersey to Florida) whereas females predominate from New York to Newfoundland. Work in the Cooper River, South Carolina, and the Altamaha River, Georgia (described in the preceding paragraph), however, does not support this hypothesis. Vladykov believed that a latitudinal change in sex composition was related to the size-differences in elvers along the coast, and he said that smaller elvers entering southern streams supposedly become males whereas the larger elvers entering northern systems probably develop into females (see the ENVIRONMENTAL REQUIREMENTS section for alternate explanations). As with freshwater-saltwater variations in the sex ratio, Dolan and Power (1977) suggested that latitudinal variations were not well documented. They stated that the apparent geographic distribution of sex in the American eel could

During the leptocephalus stage, the larvae grow and are transported by ocean currents. Larvae collected by Schmidt (1925) were 7 to 8 mm long in February, 20 to 25 mm in April, 30 to 35 mm in June, 40 mm in July, 50 to 55 mm in September, and 60 to 65 mm by the end of the first year of life. The longest leptocephalus collected by Vladykov and March (1975) was 69 mm.

Vladykov and March (1975) suggested that larval A. rostrata may spend more than 1 year in the sea. Limited evidence also suggests that some eels remain in the leptocephalus stage for more than 1 year. Smith (1968) reported a 50-mm leptocephalus near the spawning grounds during April. This larva was too long to have been spawned in the immediate season (Fahay 1978).

The Northern Equatorial Current and the Gulf Stream transport larvae northward along the eastern seaboard of North America. Sampling has shown that larvae are abundant in the Florida Straits and in the area between Bermuda and the Bahamas from April through August (Smith 1968), and Eldred (1971) found A. rostrata leptocephali in the Gulf of Mexico and Yucatan Straits, but mechanisms by which the larvae are dispersed into the Gulf of Mexico and southward to the coast of South America have not been determined.

Glass Eel Stage

During the pelagic phase, leptocephali reach a size and physiological state at which they begin to metamorphose. The early stages of this transition involve: (1) shrinkage in size and weight, primarily due to a reduction in water content; (2) changes in the configuration of the head and jaws; and (3) accelerated development of the digestive system (Fahay 1978). After these changes occur, the eels are similar in overall morphology to yellow eels, but they lack external pigmentation and are called "glass

eels." Glass eels actively migrate toward land and freshwater, and as they approach coastal areas, external pigmentation develops and the body becomes uniformly dark brown. At this stage, metamorphosis is complete and the eel is now called an elver.

Elver Stage

Most elvers move into coastal areas, estuaries, and up freshwater rivers in the late winter or early spring. Vladykov (1966) suggested that elvers generally arrive in southern estuaries earlier and at smaller sizes than in the north, but catch records indicate considerable overlap in the timing of shoreward movements along the Atlantic coast. Such movements have occurred during April in Narragansett Bay and near Washington, D.C.; February and March in Delaware; January in Long Island Sound and Rhode Island estuaries; off Nova Scotia in April, and the Bay of Fundy in summer (Fahay 1978). In the South Atlantic, migrating elvers have been collected during January in Florida and South Carolina and during January through May, with peak catches in March and April, in North Carolina (Smith 1968; Hornberger 1978, cited by Sykes 1981; Sykes 1981). Elvers moving into South Atlantic estuaries and rivers typically are 46 to 60 mm long. Helfman and Bozeman (unpublished MS.³) collected 49- to 56-mm glass eels from the Altamaha River Estuary, Georgia, in late February; daily growth rings on the otoliths showed 250 to 300 days of age.

Small numbers of elvers regularly arrive in estuaries in the fall, and Fahay (1978) suggested that these

³Growth rates of American eels in a Georgia estuary. G. S. Helfman and E. L. Bozeman, Department of Zoology and Institute of Ecology, University of Georgia, Athens, GA 30602. Submitted to U.S. Natl. Mar. Fish. Serv. Fish. Bull.

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16. Abstract (Limit: 200 words) Species profiles are literature summaries of taxonomy, life history, and environmental requirements of coastal fishes and aquatic invertebrates. They are prepared to assist with impact assessment. The American eel, <u>Anguilla rostrata</u> , is an ecologically and economically important catadromous species that occupies freshwater streams, rivers, brackish estuaries, and the open ocean during various phases of its life cycle. Adult eels apparently spawn in the Sargasso Sea, and ocean currents transport the developing larvae northward until the young metamorphose into juveniles capable of swimming shoreward and moving upstream into coastal areas, estuaries, and rivers. Developing eels commonly remain in freshwater or brackish areas for 10-12 years before migrating to spawn. American eels tend to be bottom-dwellers and feed on a variety of fauna that occupy the same habitats. Eels occupy areas having wide ranges of temperature, salinity, and other environmental factors, suggesting broad tolerance limits, but few studies of requirements have been reported. Salinity patterns and water currents created by river discharges into coastal areas apparently provide the gradient that cues shoreward migration of juvenile eels. Alteration of patterns of freshwater inflows to estuaries and bays could affect upstream migrations.			
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