

Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current systems

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Abstract

Specimen and station data for 2114 larval and postmetamorphic American eels (*Anguilla rostrata*) were compiled from North American ichthyoplankton collections and combined with data on 2359 specimens collected by Schmidt (1925, 1935) in his classic studies of North Atlantic eels. We have analyzed these data in light of current physical oceanographic knowledge to provide new insight into spawning and larval migration of the American eel. In addition 932 records of European eel (*A. anguilla*) larvae were compiled from North American collections.

Mean myomere counts for American and European eel larvae from North American collections were 106.84 ± 0.032 S.E. and 114.52 ± 0.047 S.E. Discrepancies in the literature on myomere frequency distributions of leptocephali are the result of faulty counting techniques.

Analysis of specimen phase (leptocephalus, metamorphosing leptocephalus, glass eel) and total length relative to date of collection suggest that the peak of spawning of the American eel occurs in February, that leptocephali grow rapidly at about 0.24 mm per day until October when growth slows or stops, and that the majority of leptocephali metamorphose to the glass eel phase at a length of 55-65 mm and an age of 8-12 months.

The spatial distribution of leptocephali of various size classes and the spatial distribution by bi-monthly periods were examined in relation to oceanic water mass distributions and current systems. Nearly all of the spawning of American eels must occur east of the Bahamas and north of Hispaniola, though limited spawning in the Caribbean Sea cannot be ruled out. A positive correlation may exist between the distribution of American eel spawning, as indicated by the area of occurrence of small larvae, and the Subtropical Underwater. This shallow, warm, high-salinity water mass is thought to form to the east in the area of European eel spawning. Transport of American eel leptocephali from the spawning area into the Gulf Stream system is a gradual process which may be explained as passive transport based upon known surface currents. An active transport mechanism seems to be necessary for larval detrainment on the continental side of the Gulf Stream because advection of Gulf Stream Water into the Continental Slope Water is limited in volume. Apparent patterns of continental abundance of American eels may thus be the result of a two-stage migratory process.

Introduction

Ancillary to his study on the breeding place of the European eel, *Anguilla anguilla*, Schmidt (1922, 1925) reported on the distribution and biology of American eel, *Anguilla rostrata*, leptocephali. He concluded that the American eel spawns during the late winter in the area north of the West Indian Islands, that the leptocephalus phase lasts for approximately one year, and that metamorphosis to the glass eel

phase occurs at a smaller size than is the case for the European eel. Though Schmidt's suppositions may be correct, they were founded on data which were limited spatially and temporally in areas likely important in the migration of American eel leptocephali (Vladykov, 1964).

Schmidt presented few data to substantiate his conclusions concerning the American eel. Therefore, later studies of American eel leptocephalus distribution, which presented new data (Smith, 1968; Vladykov & March, 1975; Kleckner & McCleave, 1980), were hampered by the inability to build upon his data base. Tabulation of Schmidt's data for both Atlantic eel species by J. Boëtius (Boëtius & Harding, 1985) has resolved this problem.

Our analysis of these historical records combined with new collections of American eel leptocephali has allowed us to verify and refine Schmidt's conclusions on the larval biology of this species. Furthermore, recent advances in descriptive physical oceanography, which have enhanced our understanding of surface circulation patterns in the North Atlantic Ocean, Caribbean Sea and Gulf of Mexico, have made possible consideration of potential transport mechanisms utilized by American eels during their denatant migration to the continental slope. Schmidt (1925) and Kleckner *et al.* (1983) have indicated that the initial transport of leptocephali from the spawning area is by means of passive drift with the surface flow. Areas of non-correlation between patterns of larval spatial and temporal distribution and patterns of surface current circulation are used to tentatively suggest at what point the mechanism of leptocephalus transport changes from passive drift to active migration.

This paper is based on all Atlantic eel data available to us from North American and European sources as of 1 June 1981 including the tabulations of Boëtius. We have limited our presentation to the American eel, except in analyses of myomere frequencies and plots of collections positive for European eels but negative for American eels. The latter aid in the interpretation of American eel distribution patterns.

Specimen and station data for both Atlantic eel species found in North American oceanographic collections are listed in this volume (Kleckner *et al.* 1985).

Material and methods

Sources of material

Specimens or specimen data and station data were provided by the following institutions and individuals (* = collections from which we identified and measured the specimens):

- 1.* Midwater collections of the Woods Hole Oceanographic Institution housed at the Fish Department, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
- 2.* Miscellaneous collections held by the Fish Department, Museum of Comparative Zoology, Harvard University.

- 3.* U.S. National Marine Fisheries Service, Marine Resources, Monitoring, Assessment and Prediction Program collections, Northeast Fisheries Center, Narragansett Laboratory, Narragansett, Rhode Island, U.S.A.
- 4.* Canadian Department of Fisheries and Oceans, Scotian Shelf Ichthyoplankton Program and Bay of Fundy Herring Program collections, Huntsman Marine Laboratory, St. Andrews, New Brunswick, Canada.
5. Dr. J. Boëtius, The Danish Institute for Fisheries and Marine Research, Charlottenlund, Denmark. Dr. Boëtius provided transcriptions of the J. Schmidt collection data.
- 6.* Dr. J.W.H. Hain, Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island, U.S.A.
- 7.* Dr. T.L. Hopkins, Department of Marine Science, University of South Florida, St. Petersburg, Florida, U.S.A.
- 8.* Dr. W.H. Krueger, Department of Zoology, University of Rhode Island, Kingston, Rhode Island, U.S.A.
- 9.* Dr. J.H. Power, Rosentiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida, U.S.A.
10. Dr. D.G. Smith, Marine Biomedical Institute, The University of Texas Medical Branch, Galveston, Texas, U.S.A.

Data were taken from the following publications: Tåning (1938), Eldred (1968 & 1971) and Smith (1968). Dr. Smith kindly provided further station data for the collections used in his publication.

Most of the Woods Hole Oceanographic Institution collections reported by Vladykov & March (1975) were reexamined. Some of this material is missing. We include in our study only those collections and specimens presently housed at the Museum of Comparative Zoology, Harvard University.

Species, phase and size determinations

Identifications, counts and measurements which we made were done as follows. Identification of Anguillidae followed Smith (1979). Identification of American and European eel species was based on counts of myomeres. Anteriorly, all myomeres were counted including the incomplete epaxial myomeres of the branchial region. Caudally, myomeres were difficult to differentiate in smaller specimens. Spinal ganglia, which caudally appear to underlie the myosepta, were used to differentiate myomeres in this region. Beginning with the space between the second and third from the last ganglia, adjacent spaces between ganglia were counted anteriorly until the separate myomeres became distinct.

Anguillidae with 102 to 110 myomeres were classified as *Anguilla rostrata*; those with 112 to 119 myomeres were classified as *A. anguilla*. Anguillidae with 111 myomeres (5 specimens) were excluded from our analyses.

Developmental phase was assigned following Tesch (1977; his Table 2).

Specimen total length was measured from the anterior tip of the teeth (leptocephali) or mandible (metamorphosing leptocephali and glass eels) to the distal end of the caudal fin rays. Total length is approximately 2 to 3% longer than

standard length as measured by Smith (1968) (Tesch, personal communication). We have adjusted the standard length measurements listed in Smith (1968) by a factor of 1.025.

Total length versus day of collection analyses

The general linear models procedure was used to compute linear regression statistics of specimen length on day of collection (based on 365 day year) for two groups of *A. rostrata* leptocephali and for *A. rostrata* glass eels. One group of *A. rostrata* leptocephali included only 0-group specimens collected between the beginning of the year and 15 October (day 287). The second group included 0-group leptocephali collected after 15 October (day 288 to 365) and 1-group leptocephali. 1-group leptocephali were defined as specimens exceeding 39 mm TL collected between 1 January and 20 April (days 1 to 110 + 365) and as specimens exceeding 49 mm TL collected between 21 April and 15 June (days 111 to 166 + 365).

Analyses of spatial distribution

Plots of spatial distribution were drawn by a computer graphics system. Samples negative for both *A. rostrata* and *A. anguilla* were omitted from analysis because negative samples could result from improper sampling or sorting technique (see next section for discussion). We have used samples positive for *A. anguilla* but negative for *A. rostrata* to further define the limits of distribution of *A. rostrata* leptocephali. This method was used only when the expected length range for *A. rostrata* at that time of year fell within the length range of the *A. anguilla* in the collection.

Limitations of the data and sources of error

The size and abundance of specimens in a collection may be influenced by gear selectivity, net avoidance, depth range sampled and trawl pattern (horizontal, oblique, etc.). The care with which leptocephali are sorted from a sample of zooplankton may also bias results. Variability in net type, trawl pattern and sorting technique employed in gathering these collections precludes their use in detailed analyses of the relative abundance of American eels. Therefore we limit our analyses to the spatial and temporal distribution of leptocephali without comment on abundance except when comparing collections made by a single research group using only one type of net.

Length measurements of fixed and preserved leptocephali are underestimates (F.-W. Tesch, personal communication). The specimen total length measurements used in this study have not been adjusted to account for shrinkage, because we do not know the fixation and preservation histories of most of these collections.

Results

The data base

Specimen and station data for 2114 American eels and 932 European eels found in North American ichthyoplankton collections and 2359 American eels collected by Schmidt west of 40°W longitude were used in our study. The American eels include 4316 leptocephali, 12 metamorphosing leptocephali and 145 glass eels. They were collected at 486 stations in the North Atlantic Ocean, Gulf of Mexico and Caribbean Sea.

Myomere frequency distribution

Myomere counts for *Anguilla* leptocephali in the North American collections ranged from 102 to 119 with a bimodal frequency distribution peaked at 107 and 114 to 115 myomeres (Table 1). The antimode of this distribution at 111 myomeres includes five specimens. Specimens with 102 to 110 myomeres, which we classified as *A. rostrata*, had a mean myomere frequency of 106.84. Specimens with 112 to 119 myomeres, which we classified as *A. anguilla*, had a mean myomere frequency of 114.52. The myomere frequencies did not vary significantly with total length in either American eel leptocephali ($F_{(1,1925)} = 0.78$; $P < 0.05$) or European eel leptocephali ($F_{(1,927)} = 0.73$; $P < 0.05$).

Table 1. Total numbers of myomeres for *Anguilla* leptocephali found in North American collections.

Total number of myomeres	Number	% of group	Group statistics
<i>Anguilla anguilla</i>			
119	4	0.4	
118	15	1.6	
117	67	7.2	Mean = 114.52
116	132	14.2	S.E. = 0.047
115	239	25.7	N = 929
114	238	25.6	
113	164	17.7	
112	70	7.5	
<i>Anguilla</i> sp.			
111	5	—	
<i>Anguilla rostrata</i>			
110	44	2.3	
109	172	8.9	
108	377	19.6	
107	609	31.6	Mean = 106.84
106	409	21.2	S.E. = 0.032
105	230	11.9	N = 1927
104	67	3.5	
103	12	0.6	
102	7	0.4	

Length and phase versus day of collection

American eel leptocephali ranged from 7 mm to 70 mm in length (Fig. 1A). Only 26 leptocephali were in the 7 to 10 mm size range. These specimens were collected between 13 February and 27 April. Leptocephali greater than 45 mm long were taken during all months. The presence of two year classes of leptocephali from February through mid-June is indicated by a bimodal distribution in specimen length. This distribution is obscured during June as 0-group leptocephali grow to exceed 45 mm. Therefore, we have assigned all but one of the leptocephali collected after 15 June to the 0-group year class. The 70 mm leptocephalus collected on 1 August (collection number RHB 2612) was included with the 1-group year class.

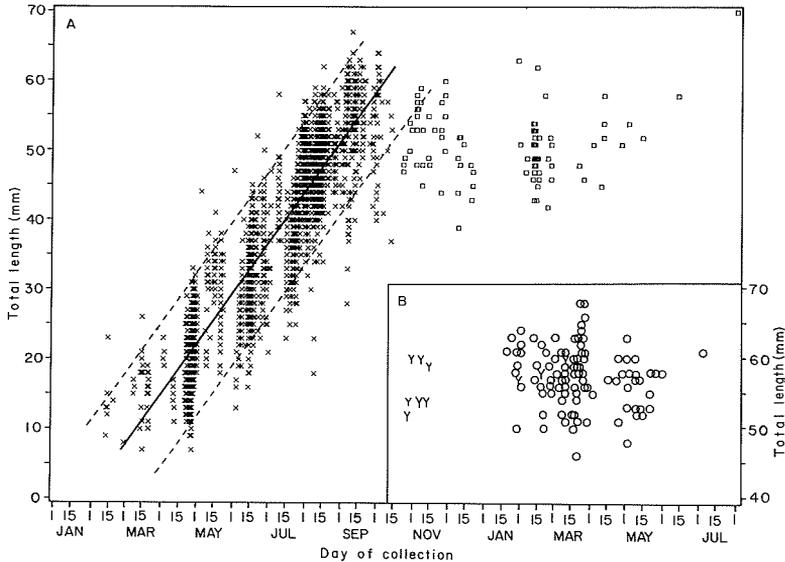


Fig. 1. Total length of *Anguilla rostrata* in relation to day of collection. A, 0-group leptocephali collected between 1 January and 15 October (×), included in the calculation of the linear regression (equation 1) and associated 95% confidence area (---), and later-caught 0-group leptocephali and 1-group leptocephali (□). B, metamorphosing leptocephali (Y) and glass eels (○).

The average length of 0-group leptocephali clumped by month of collection increased until October (September mean TL = 53.1, $n = 271$; October mean TL = 53.1, $n = 27$). For 0-group leptocephali collected between 13 February and 15 October the regression of length (Y; mm TL) on day of collection (X; Julian date) is as follows:

$$Y = 0.238X - 6.569 \quad (1)$$

($F_{(1,4201)} = 1.7 \times 10^4$; $P < 0.0001$; $r^2 = 0.81$). The linear regression coefficient for 0-group leptocephali collected after 15 October combined with 1-group lepto-

cephali is not significantly different from zero ($F_{(1,95)} = 0.00$; $P < 0.05$). These specimens averaged 51.1 mm TL (standard error = 0.53; range = 39 to 70 mm).

Twelve metamorphosing leptocephali collected between 28 October and 11 March averaged 56.3 mm TL (standard error = 0.89; range = 52 to 60 mm) (Fig. 1B). The 133 glass eels collected between 20 January and 5 July averaged 57.9 mm TL (standard error = 0.34; range = 46 to 68 mm) (Fig. 1B). The linear regression coefficient based on length versus date of collection for glass eels is not significantly different from zero ($F_{(1,131)} = 2.68$; $P < 0.05$).

Spatial and temporal distribution

With one exception *A. rostrata* leptocephali were collected between 11°00'N to 42°-35'N latitude and 43°50'W to 87°00'W longitude (Fig. 2). This leptocephalus, collected at 49°43'N, 20°45'W (RHB2612), measured 70 mm TL and had 109 myomeres.

All American eel leptocephali 10 mm TL or less and all 0-group leptocephali collected during February and March were found in samples taken within a 550 km arc east of the Bahama Islands and north of Hispaniola Island (Figs 2, 3). Most collections from farther north and east (Fig. 3), which did not contain 0-group American eels, were taken with nets capable of retaining small leptocephali.

Only one April-May collection taken in the eastern Sargasso Sea between 23° to 28°N and 51° to 63°W included an 0-group American eel (Fig. 4). The numerous collections in this area were taken by J. Schmidt with nets capable of collecting 0-group leptocephali. Collections taken to the northwest and southwest in the

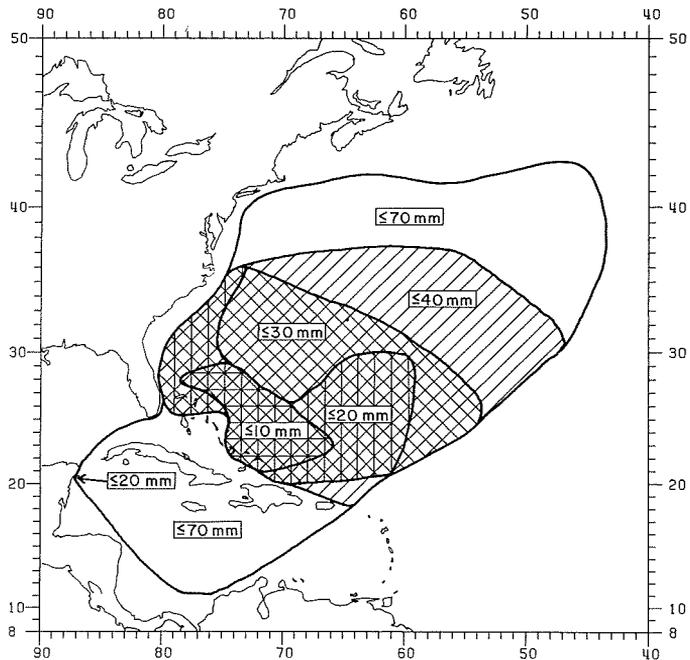


Fig. 2. Limits of the distribution of *Anguilla rostrata* of various sizes.

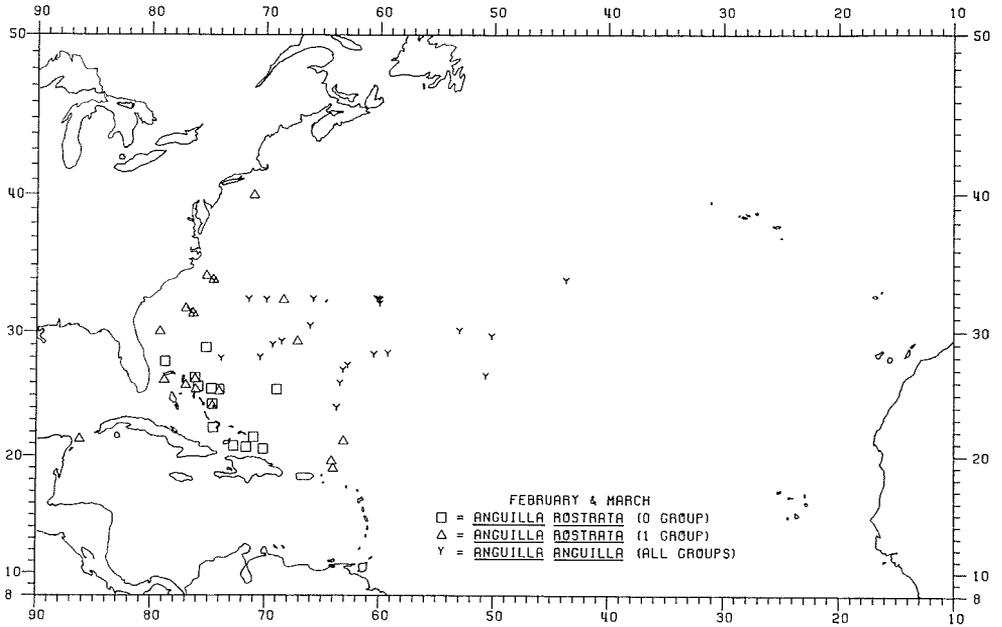


Fig. 3. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in February and March.

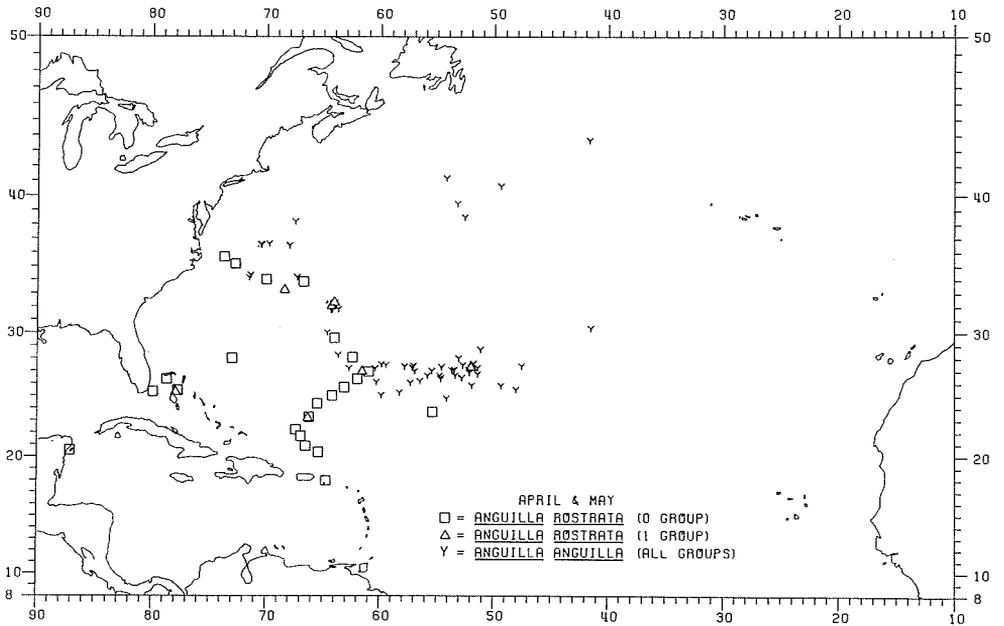


Fig. 4. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in April and May.

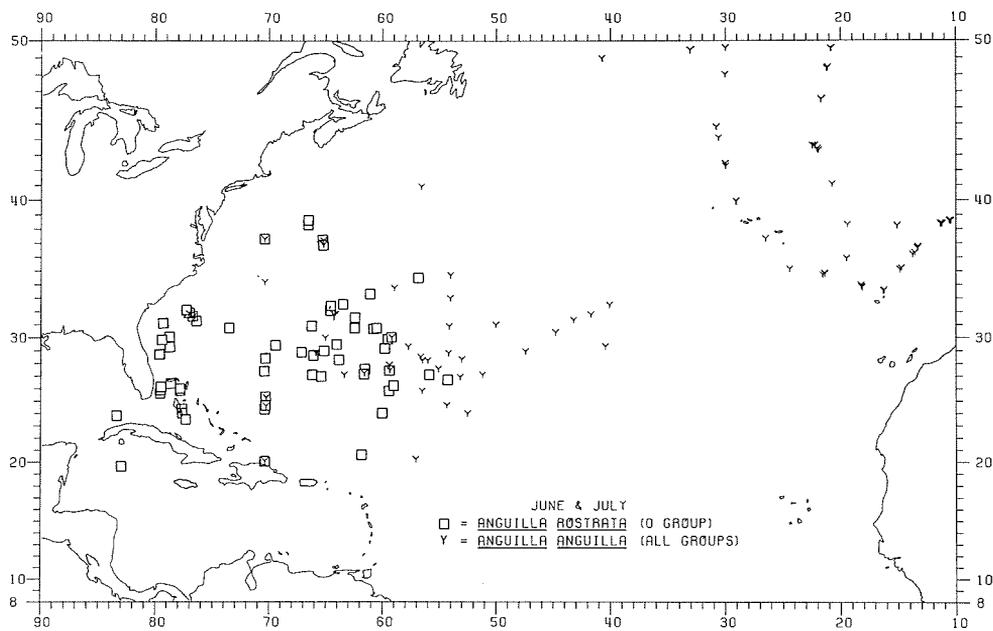


Fig. 5. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in June and July.

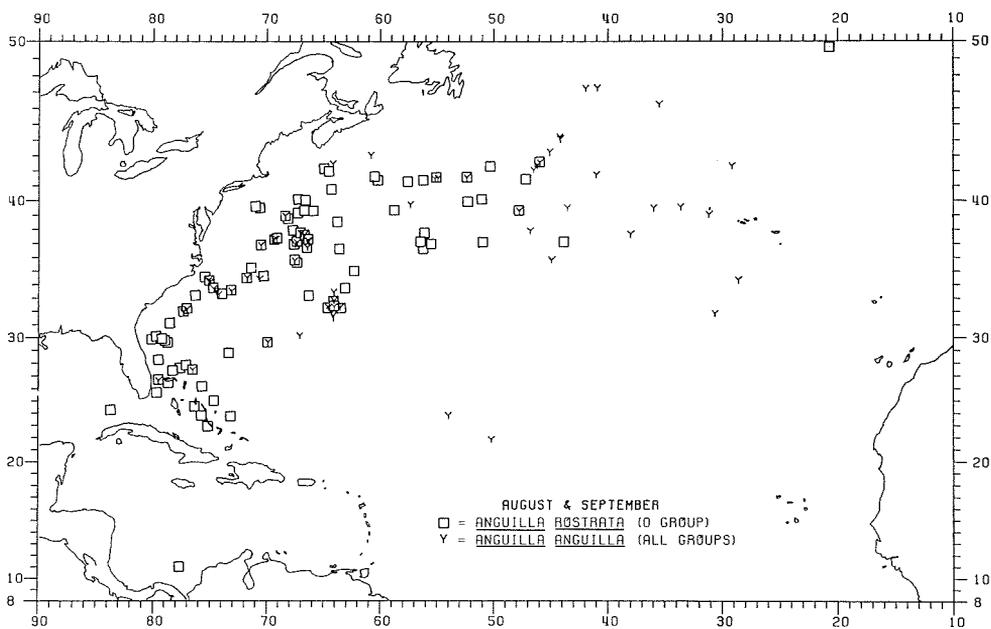


Fig. 6. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in August and September.

Sargasso Sea and in the Caribbean Current along the west shore of the Yucatan Channel, in the Straits of Florida and in the Gulf Stream to the east of Cape Hatteras included 0-group American eels. Collections taken in the area of the North Atlantic Current between 38° to 44°N and 41° to 55°W, with nets capable of collecting small leptocephali, were negative.

Collections of 0-group American eels were taken in the Caribbean, Gulf Loop, Florida and Gulf Stream Currents during June and July (Fig. 5). Too few collections were taken south of Newfoundland to define the eastern limit of 0-group American eels in the Gulf Stream. No American eels were present in collections from the eastern North Atlantic Current. Collections of 0-group American eels were taken east to 54°15'W in the southern Sargasso Sea. Northeast of Bermuda positive collections were taken east to 56°46'W.

August and September collections include American eel leptocephali from stations in the southern Caribbean Sea, Gulf Loop Current, Florida Current, Gulf Stream and North Atlantic Current (Fig. 6). American eel leptocephali were also present northwest of the Gulf Stream Current, in collections (RHB 1003, 1004, 1006, 1008, 1013 & 1503) identified as being taken in Continental Slope Water (Jahn & Backus, 1976; Backus & Craddock, 1977). Nearly all American eel leptocephali from the area of the North Atlantic Current were taken west of 43°W. The eastern-most specimen taken in RHB 2612 was probably a 1-group leptocephalus. Too few *Anguilla* positive collections were taken in the southern Sargasso Sea to define the presence or absence of American eel leptocephali.

October and November collections taken in the Caribbean Sea from south of Puerto Rico to the Yucatan Channel included American eel leptocephali (Fig. 7). American eel leptocephali were taken both inshore and offshore of the Gulf Stream south of the northeastern United States and Canadian maritime provinces, while to the south and east in the Sargasso Sea only scattered collections were positive.

The pattern of distribution for American eels in December-January collections is poorly defined because of lack of sampling (Fig. 8). While many collections taken north and south of Bermuda in the Sargasso Sea did not contain American eels, two specimens were taken well to the east near 47°30'W.

1-group American eel leptocephali occurred in widely scattered collections taken in the Caribbean Sea and western North Atlantic Ocean during February-March (Fig. 3) and April-May (Fig. 4). Many of the positive February-March collections were taken near the Bahama Islands and in the area of the Florida Current off of the southeastern U.S. coast.

Metamorphosing American eel leptocephali occurred north of the Gulf Stream between 65°42'W and 73°30'W (Fig. 9). One of these collections was taken over the continental shelf approximately 28 km from the coast. Collections taken further to the east were over the continental slope. In the Sargasso Sea metamorphosing leptocephali were taken approximately 55 km southwest of Bermuda and approximately 445 km southeast of Cape Hatteras. One specimen was taken in the Gulf of Mexico approximately 110 km north of Campeche Bank.

Glass eels were taken over the continental shelf and slope (Fig. 9). One specimen was taken in the area of the Gulf Stream northeast of Cape Hatteras.

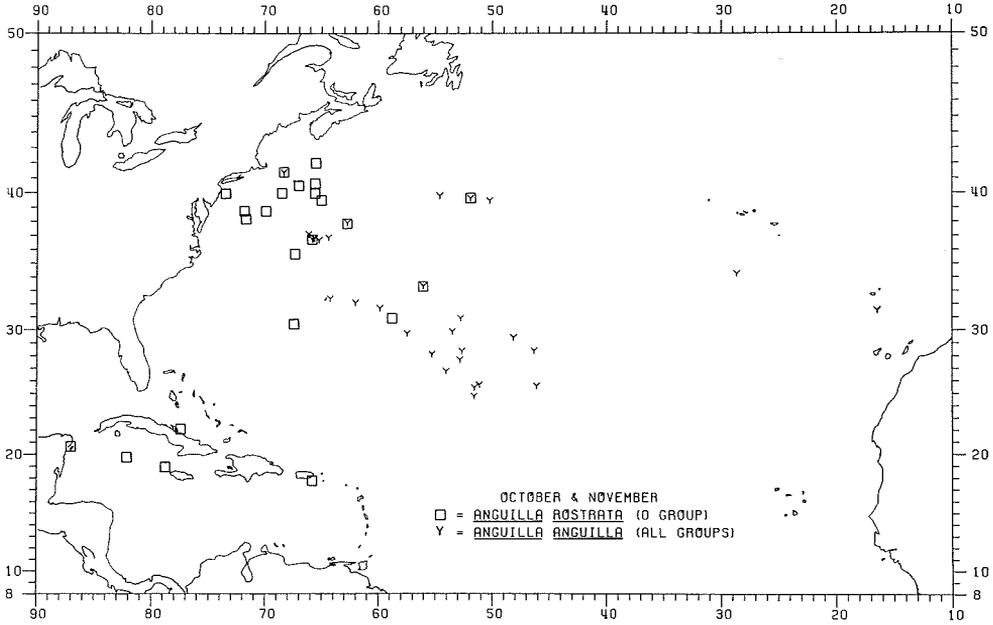


Fig. 7. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in October and November.

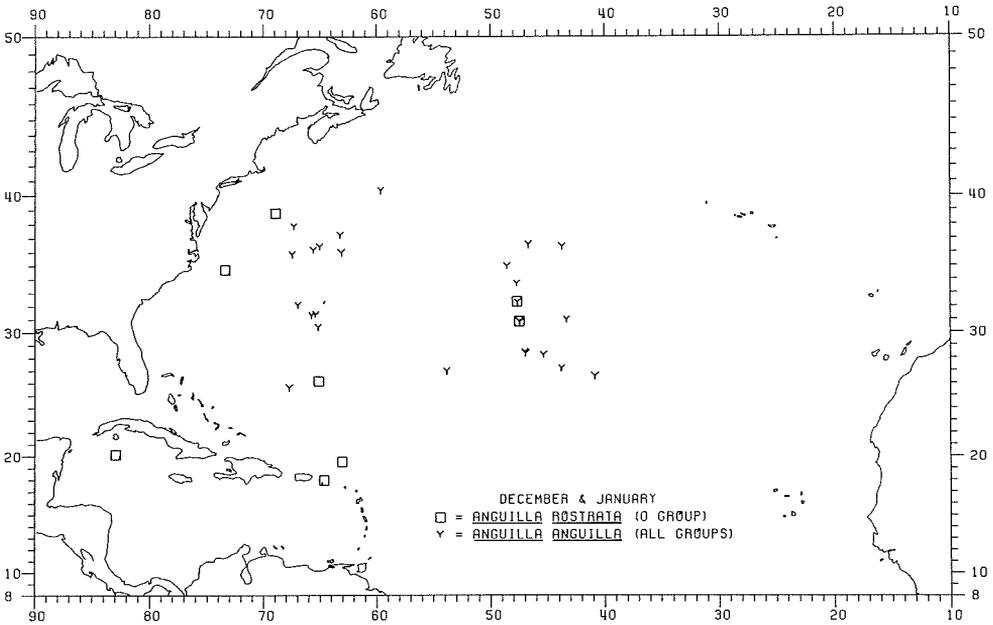


Fig. 8. Locations of collections of *Anguilla rostrata* and *A. anguilla* taken in December and January.

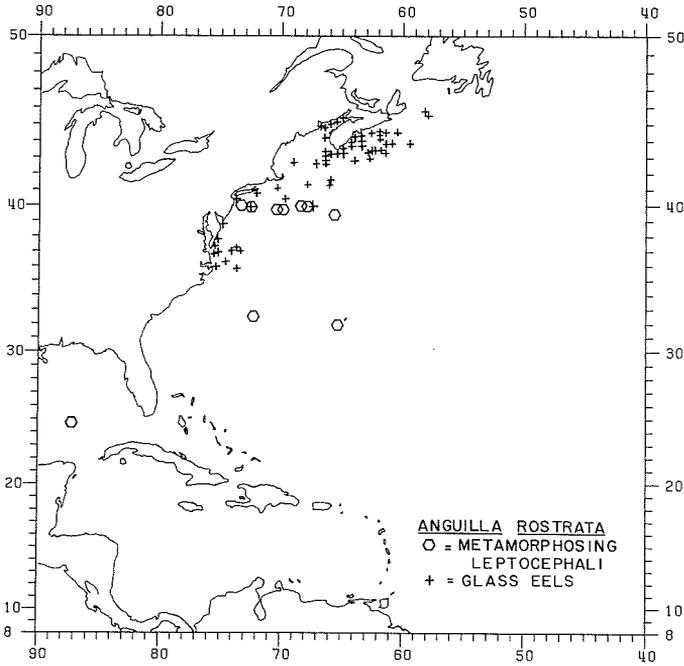


Fig. 9. Locations of collections of *Anguilla rostrata* metamorphosing leptocephali and glass eels.

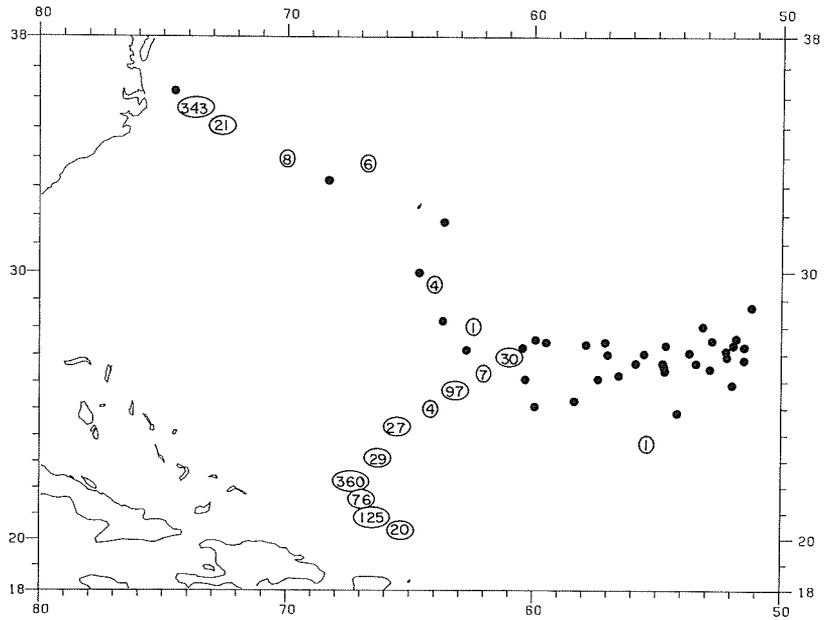


Fig. 10. Numbers of 0-group *Anguilla rostrata* leptocephali taken at Dana I and Dana II stations during April-May (● = negative station).

Sampling procedures for collections taken during the Dana I and Dana II cruises in the Sargasso Sea (Schmidt, 1929) were sufficiently consistent to permit the spatial and temporal comparison of the relative abundance and size of 0-group American eel leptocephali collected during April-May and June-July. Trawl duration for most collections was 120 min; catch totals for longer and shorter trawls were adjusted by simple proportion.

0-group American eels were considerably more abundant in the Gulf Stream and in the southwestern Sargasso Sea than in the area northwest and southwest of Bermuda during April-May (Fig. 10). Leptocephali taken in the area of the Gulf Stream (Dana 1352) were an order of magnitude more abundant and averaged 6.2 mm shorter than those taken 110 km to the southeast (Dana 1345) in the Sargasso Sea (Table 2). Collections taken inshore of the Gulf Stream (Dana 1349) did not contain any leptocephali (Schmidt, 1929). 0-group American eel leptocephali taken in nearly synoptic collections made along a transect through the southwestern Sargasso Sea also varied markedly in abundance (Fig. 10) and mean length (Table 3). Leptocephali taken at the northern end (Dana 942) and middle (Dana 946) of the transect averaged approximately 8 mm shorter than leptocephali taken in the three southern collections (Dana 949 to 951) (Table 3).

In contrast with April-May collections, collections made during June-July in the area between Bermuda and 28°N took numerous American eel leptocephali (Fig. 11). Leptocephali taken in nearly synoptic collections along an east-west transect increased in average length east and west of approximately 59°W (Table 4). Specimens at the western extreme of the transect averaged 14 mm longer than specimens taken at 59°W.

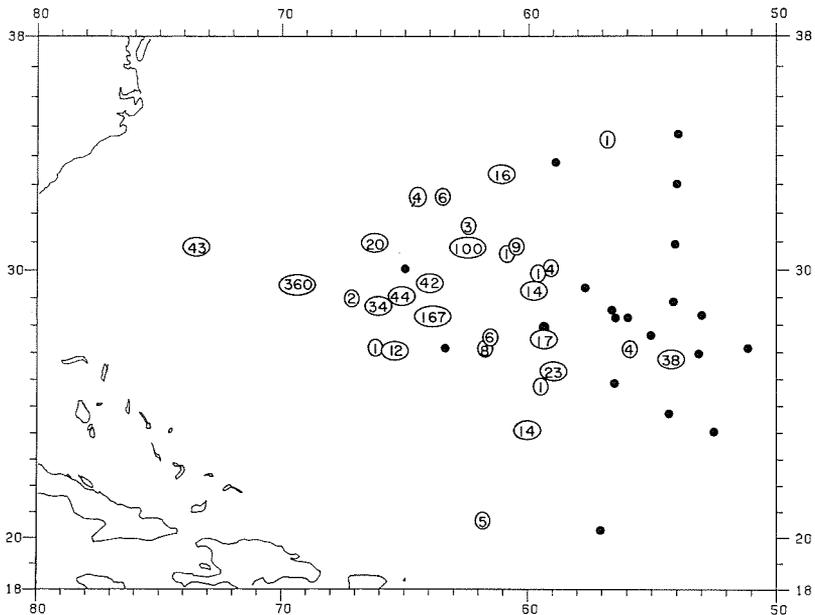


Fig. 11. Numbers of 0-group *Anguilla rostrata* leptocephali taken at Dana I and Dana II stations during June-July (● = negative station).

Table 2. Mean lengths (TL) of 0-group American eel leptocephali in nighttime Dana II collections taken between 7 and 23 May 1922.

Dana II station	North latitude	West longitude	Number of specimens	Total length (mm)	
				Mean	S.E.
1335	28°02'	62°26'	1	24	—
1337	29°36'	64°01'	4	21.8	1.797
1353	33°51'	66°43'	6	32.0	1.125
1342	34°00'	70°01'	8	32.1	0.766
1345	35°07'	72°38'	21	34.4	0.645
1352	35°42'	73°43'	343	28.2	0.156

Table 3. Mean lengths (TL) of 0-group American eel leptocephali in nighttime Dana I collections taken between 21 April and 1 May 1921.

Dana I station	North latitude	West longitude	Number of specimens	Total length (mm)	
				Mean	S.E.
942	26°57'	60°58'	30	16.1	0.675
943	26°20'	62°00'	7	23.1	1.818
944	25°40'	63°10'	97	20.8	0.353
945	25°00'	64°10'	4	19.5	1.756
946	24°20'	65°30'	27	16.1	0.629
947	23°10'	66°15'	29	18.4	1.172
948	22°14'	67°22'	360	19.5	0.268
949	21°40'	66°55'	76	23.9	0.397
950	20°50'	66°30'	125	24.4	0.324
951	20°20'	65°20'	20	24.4	0.828

Table 4. Number and mean length (TL) of 0-group American eel leptocephali in nighttime Dana I collections taken between 16 and 25 July 1920.

Dana I station	North latitude	West longitude	Number of specimens	Total length (mm)	
				Mean	S.E.
885	26°46'	54°14'	38	33.6	0.663
887	26°19'	58°58'	23	31.2	0.942
888	27°31'	61°32'	6	36.3	1.202
889	28°20'	63°50'	167	37.4	0.295
890	28°44'	66°04'	34	37.9	0.777
891	29°28'	69°25'	360	39.6	0.179
892	30°49'	73°30'	43	45.5	0.591

Discussion

The mean myomere counts of 106.84 and 114.52 for American and European eels, respectively, are lower than those of Jespersen (1942) (108.17 and 115.58), higher than those of Vladykov & March (1975) (105.13 and 111.76) and comparable with those of Schoth (1982) (106.96 and 114.68). Variation in mean myomere counts between studies is clearly due to systematic differences in counting technique. The pattern of myomere frequency distribution reported by Jespersen for the North American and European species is similar to that which we report except that the peaks of the bimodal distribution are offset by one myomere: 108 myomeres and 115 to 116 myomeres in Jespersen's study and 107 myomeres and 114 to 115 myomeres in our study. The antimode of the myomere distribution reported by Jespersen is similarly offset by +1 from that which we report (111 myomeres).

We have reexamined most of the specimens studied by Vladykov & March (1975), and myomere counts listed on their specimen vial labels were consistently lower than our recounts. The peak myomere frequencies of 105 and 111 and 112 reported by Vladykov & March for American and European eel leptocephali are respectively two and three myomeres less than we report. The antimode for the distribution reported by Vladykov & March is at 108 and 109 myomeres, two to three less than the antimode which we report. They suggest that variation between their frequencies and Jespersen's 'could be attributed to several causes: counting technique, different number of specimens, variation in size of specimens, and difference in collecting localities' (Vladykov & March, 1975; page 8). We believe that counting technique is the most probable cause of this variation.

The day of the year for peak American eel spawning is unknown though it has generally been assumed to occur during February (Harden Jones, 1968). Too few small leptocephali were taken in the collections analyzed herein to provide direct evidence of a spawning peak. The topic is discussed by Wippelhauser *et al.* (1985).

Existing growth curves for American eel leptocephali are based on few data and much speculation (Harden Jones, 1968; Tesch, 1977). Even so, the curve drawn by Tesch (1977; his Fig. 40) approximates the pattern of growth of 0-group leptocephali between February and October shown by our Figure 1 remarkably well. Our data suggests that an average American eel leptocephalus undergoes a period of rapid growth of approximately eight months duration beginning in February and ending in October during which its length increases at a rate of about 0.24 mm per day.

The following points lead us to suggest that the length at which most American eel leptocephali undergo metamorphosis to the glass eel phase is between 55 mm and 65 mm TL: 1) the average lengths of metamorphosing leptocephali (56.3 mm TL) and glass eels (57.9 mm TL), 2) the few leptocephali greater than 64 mm TL, and 3) the reduction in the frequency of occurrence of leptocephali greater than 55 mm TL in collections taken after mid-November. We cannot state with certainty the minimum size at which metamorphosis takes place due to the possibility of length reduction during metamorphosis, as occurs in the European eel (Schmidt 1909a).

The presence of leptocephali 60 to 64 mm TL in September collections, their absence in October, and the first appearance of metamorphosing leptocephali late in October lead us to suggest that some American eel leptocephali may initiate metamorphosis early in October. The collection of metamorphosing leptocephali into mid-March suggests either that metamorphosis to the glass eel phase requires an extended period for complete transformation, as suggested by Schmidt (1906), or that leptocephali initiate metamorphosis as they become developmentally competent or respond to an environmental cue from October to March. Again assuming similarity between American and European species, the observations reported by Grassi (1896) of European eel leptocephali held in an aquarium undergoing metamorphosis in about one month, lead us to believe that metamorphosis in American eels may be initiated over an extended period.

The rate of growth of leptocephali not undergoing metamorphosis in the fall must slow dramatically during the fall and winter. There is no increase in length of leptocephali collected after 15 October and there are no 1-group leptocephali less than 40 mm TL present during the winter from which the 40 to 60 mm TL leptocephali, present throughout the winter, could be recruited.

Schmidt (1925) believed that American eel leptocephali represented only a single year class. Vladykov & March (1975) suggested that two year classes were present in their collections. Our results demonstrate the presence of two year classes from February to August. However, the few 1-group leptocephali present lead us to believe that most American eels undergo metamorphosis at about one year old.

According to Schmidt (1925) the continental separation of the American and European eel species requires metamorphosis of the former after only one year. The presence of some 1-group leptocephali in our collections contradicts this hypothesis and helps to explain in part the finding of Boëtius (1976, 1980) that the American species may represent up to 0.4% of Danish elver catches. The 70 mm TL American eel leptocephalus collected in RHB 2612 west of the English Channel at 20°45'W might have arrived in European continental waters had it not been intercepted.

The addition of records for 2114 American eels to the data base used by Schmidt (1935) has created two important expansions in the spatial distribution limits presented for leptocephali (his Fig. 3). First, the specimen collected in RHB2612 at 49°-43'N, 20°45'W (Fig. 6) extends the limit for leptocephali of all sizes about 1600 km to the east. Second, the collection of leptocephali 11 mm to 17 mm TL over the Caribbean continental shelf of the Yucatan Peninsula extends the range of the two smallest size groups outlined by Schmidt (≤ 15 mm and ≤ 30 mm) from the southwestern Sargasso Sea to the western Caribbean Sea (Fig. 2). Kleckner & McCleave (1982) considered the possible origins of these small leptocephali.

The reported presence of adult American eels in Guyana and Surinam (Schmidt, 1909b) and the collection of 38 adults in Trinidad led Vladykov (1964, p. 1528) to conclude that 'the true spawning place for *A. rostrata* is not in the area outlined by Schmidt (1922) but much further south.' While the data available at present are not adequate to resolve the occurrence of limited spawning south of the southwestern Sargasso Sea, we do believe them adequate to state that the majority of

spawning occurs north of the Bahamas/Antilles arc. By limiting the outline of the smallest size group represented to specimens ≤ 10 mm TL (Fig. 2), we have significantly reduced the probable area wherein most American eel spawning occurs. This reduction is supported by the recent collection of American eel leptocephali ≤ 7 mm TL in or near this area (Schoth & Tesch 1982; Wippelhauser *et al.* 1985). These latter studies, which were conducted during the spawning period, reported many negative stations, or stations with only larger leptocephali present, outside the ≤ 10 mm TL distribution limit outlined in Fig. 2. Furthermore, most American eel leptocephali enter the Gulf Stream System north of the Straits of Florida (Kleckner & McCleave, 1982). If the principal spawning area was located to the south, the majority of leptocephali would enter the Gulf Stream System by way of the Caribbean and Gulf Loop Currents. In the rest of this discussion references to 'the spawning area' refer to the region within or near the ≤ 10 mm limit outlined in Fig. 2.

The Bahama/Antilles Arc forms the southern and western boundaries of the American eel spawning area in the Atlantic. Hydrographic features may form its northern boundary. Ekman (1932) suggested that the thermal characteristics of the upper 300 m of the water column might be used by migrating European eels to identify their spawning area. Specifically, he noted a positive correlation between the spawning area outlined by Schmidt (1922) and 18-19°C isotherms at depths of 200-300 m. Schmidt (1935, p. 9) stated that 'all over the world the small Eel (*Anguilla*) larvae seem to require a high salinity (and temperature) in order to thrive.' We (Kleckner *et al.* 1983) have pointed out that the northern limit of American eel spawning is an area in which thermal fronts are found during the winter and spring (Voorhis & Hersey, 1964). The fronts separate distinct surface water masses with high temperature and salinity water to the south and seasonally cooled, low salinity water to the north (Katz, 1969). The southern water mass has the temperature-salinity correlation (Katz, 1969, his Fig. 8) of the Subtropical Underwater (Gunn & Watts, 1982, their Fig. 1), a shallow (<200 m), warm (>18.2°C), salinity maximum water (>36.6‰) which is formed to the east of the American eel spawning area. The European eel spawning area (Schmidt, 1935, his Fig. 1) lies within the area of Subtropical Underwater formation (Worthington, 1976, his Fig. 35). It seems likely that a thermal or chemical characteristic of this water mass acts as a cue to migrating adult eels of both species triggering the cessation of migration and the initiation of spawning.

We are unable to associate geographic or hydrographic features with the eastern limit of American eel spawning. It is possible that this limit is controlled by a directional orientation mechanism utilized by migrating adults in attaining the spawning area rather than by a mechanism involved in the identification of the spawning area. This seems to be a fruitful area for comparative laboratory studies between the two species.

Initial transport of leptocephali from the spawning area is likely by mean of passive drift (Schmidt 1925; Harden Jones 1968; Kleckner *et al.* 1983). The Antilles Current, depicted as a northwesterly flow outside of the Bahama/Antilles arc (Wüst, 1924), might form an avenue for this transport. However, questions

have been raised concerning the width, strength and persistence of the current (Iselin, 1936; Day, 1954; Gunn & Ingham, 1977). A recent analysis of July-August and January-February hydrographic data from an extensive grid of stations east of the Bahamas and north of the Antilles revealed that a well developed northwestward surface flow was present during the winter and absent during the summer (Gunn & Watts, 1982). The winter current, which paralleled the island arc between at least 71° and 78°W, had a calculated velocity of 10 to 20 cm s⁻¹ at a depth of 175 m and was 200 km wide. If this flow continues during the spring it would transport American eel leptocephali towards the Gulf Stream. Limited sampling immediately northeast of the Bahama/Antilles arc during April-May (Fig. 4) and June-July (Fig. 5) prohibits direct determination of the significance of this route.

Indirect evidence for significant northwesterly transport from the spawning area was provided by a simulation model based on the advection-diffusion equation and surface currents calculated on a monthly basis from ship's drift observations (Power & McCleave 1983). Spatio-temporal patterns of concentration were generated for 'cohorts' of leptocephali started as point sources in the presumed eel spawning area. The model predicted that a concentration of leptocephali is transported gradually to the northwest during the spring to form a large patch offshore of the Florida Current northeast of the Bahamas during the summer. This prediction is supported in part by an increase in the number of eel larvae in the Florida Current between the Straits of Florida and Cape Hatteras and a concentration of American eel leptocephali found east of the Florida Current between 31° and 32°N (Kleckner & McCleave, 1982).

Not all leptocephali are transported to the northwest from the spawning area. Dana collections made in April-May (Fig. 10) and June-July (Fig. 11) show a dispersal of 0-group American eels to the east and north in the southern and central Sargasso Sea. Clines in the mean TL of leptocephali taken in nearly synoptic collections along transects leading away from the spawning area (Tables 2, 3 & 4) suggest that the forces driving this dispersal can function for extended periods. Transport to the north and northeast in this area is not predicted by the generalized North Atlantic surface circulation shown in Sverdrup *et al.* (1942, his Fig. 187), which depicts a southwesterly surface flow north of the Antilles Current. Similarly, Worthington's (1976) scheme for the North Atlantic circulation calls for the recirculation of Gulf Stream system water exceeding 17°C in a southwesterly direction through the area.

It is possible that northerly and easterly dispersal of leptocephali from the spawning area may be driven by localized currents generated by mesoscale eddies. Gunn & Watts (1982, p. 9) stated that during the summer 'eddy variability characterized the circulation of the upper level waters (<500 m depth) away from the Antilles Arc.' Some evidence exists for a more persistent flow in the central Sargasso Sea. Current vectors measured at a depth of 100 m on a permanent mooring 460 km south of Bermuda averaged about 10 cm s⁻¹ to the north over a period of 87 days (Day & Webster, 1965, their Fig. 1). This was followed by an increase in current speed and shift in direction to the east and then south, possibly created by

the movement of an eddy into the area. Similarly, a free-drifting buoy exhibited a looping trajectory of 200 km diameter in an area centered about 300 km southeast of Bermuda (Richardson, 1981).

Computer simulations of leptocephalus drift for specimens originating along 27°N at 66°, 69° and 72°W showed a strong northwesterly transport component, as in simulations begun closer to the Bahama/Artilles arc. In addition simulations with northern origins had a gradual northeasterly transport component that was lacking in the southern series of simulations (Power, personal communication).

The occurrence of American eel leptocephali in collections from the Bahama/Antilles archipelago, Caribbean Sea, Gulf of Mexico, and Straits of Florida (Figs 3-8) suggests that they may also be transported to the west and southwest from the spawning area. Recovery amongst the Bahama Islands of drift bottles released up to 800 km to the northeast (Day, 1954) indicates that leptocephali could be transported into the islands from the spawning area. Surface currents through the Windward and Mona Passages (Metcalf *et al.*, 1977; Grant & Wyatt, 1980; Roemmich, 1981; Gunn & Watts, 1982; Morrison & Nowlin, 1982) could then transport leptocephali into the Caribbean Sea. Leptocephali transported by this route could be dispersed along the Caribbean coast by eddies (Molinari *et al.* 1981) and coastal counter-currents (Wüst, 1964; Brucks, 1971; Duncan *et al.*, 1977) or they could be carried by the Caribbean Current through the Yucatan Channel into the Gulf of Mexico and the Gulf Loop Current. The former route might possibly carry leptocephali along the north coast of South America towards Guyana and Surinam (Harden Jones, 1968). The latter route is certainly the transport mechanism for American eels distributed along the Gulf Coast of the United States.

The Gulf Loop Current, which flows out of the Gulf of Mexico as the Florida Current, provides a likely source of leptocephali collected in the Straits of Florida (Smith, 1968; Kleckner & McCleave, 1982). Leptocephali may also be transported into the Straits of Florida from the Bahama/Antilles archipelago by currents through the Old Bahama Channel and then Nicholas and Santaren Channels north of Cuba (Wennekens, 1959) or through the Northwest Providence Channel south of Grand Bahama Island (Richardson & Finden, 1967). Smith (1968) stated that the earliest record for 0-group American eel leptocephali in the Straits of Florida was April 2. We note that all April 2 samples were taken more than 100 km east of the Straits of Florida in Tongue of the Ocean east of Andros Island (Smith, 1968, Table 1). Our data indicate that 0-group leptocephali were first taken in the Straits of Florida on May 4 by Tursiops 107 recorded by Smith (1968).

It is likely that 0-group American eels enter the Gulf Stream system north of the Straits of Florida by early April; four leptocephali 10-16 mm TL were taken north of Little Bahama Bank less than 75 km east of the Florida Current on March 21 in R/S Bache collection 10208 (Harding & Boëtius, this volume). By May they are abundant in the Florida Current east of Cape Hatteras (Table 2, Fig. 10). Collections made during August along a series of transects crossing the Florida Current revealed a 9-fold increase in the abundance of American eels in the current between the northern Straits of Florida and Cape Hatteras (Kleckner & McCleave,

1982). Most of this increase occurred north of 30°N, coinciding geographically with the predicted increase in the volume transport of the Florida Current between Jacksonville, Florida and Cape Hatteras (Knauss, 1969; Richardson *et al.*, 1969; Richardson & Knauss, 1971; Worthington, 1976; Stommel *et al.*, 1978).

Though American eels are common in the Gulf Stream between Cape Hatteras and the Southeast Newfoundland Rise (located near 38°N, 45°W) during August and September (Fig. 6), collection techniques were too variable to allow comparison of their abundance along its course. This problem is compounded by variability in the position of the Gulf Stream created by the formation of meanders (Hanson, 1970) and eddies (Parker, 1971; Saunders, 1971).

American eel leptocephali still in the Gulf Stream as it nears the Southeast Newfoundland Rise will likely be carried on by one of the three branches of the Gulf Stream system (Mann, 1967; Clark *et al.*, 1980; Richardson, 1981). One branch, which forms the North Atlantic Current, flows first to the north and then east passing north of the Azores. The 70 mm TL American eel collected in RHB 2612 was probably transported by this current. A second branch flows to the southeast passing south of the Azores and a third branch recirculates to the southwest along the southern edge of the Gulf Stream.

The fast flowing currents of the Gulf Stream system have been considered as both transport mechanism (Harden Jones, 1968) and as barriers (Vladykov, 1964) in the migration of American eels from the spawning area to the coast. In reference to the Gulf Stream currents, Vladykov (1964; p.1527) stated that 'they must interfere greatly with the normal distribution of the American Eel larvae. To reach North America, *A. rostrata* leptocephali must somehow cross the Gulf Stream without being swept away into the northeast Atlantic.' To say that these currents 'interfere greatly' with this distribution is to suggest that the species has not adapted its life history to a current system which has existed for at least 18 thousand years (McIntyre *et al.*, 1976). It is intuitively obvious that mechanisms exist whereby American eels cross the currents of the Gulf Stream system and that these currents will influence the continental distribution of American eels. In the remainder of this paper we address these topics.

Between the northern Straits of Florida and the New England Seamounts (extending southeast from Cape Cod) the Gulf Stream system currents average about 100 km wide and have maximum near surface speeds of about 160 to 250 cm s⁻¹ (Richardson *et al.*, 1969; Richardson, 1981). East of the New England Seamounts the maximum current speed slows to about 50 cm s⁻¹ and large amplitude meanders appear to spread the current to a width up to 350 km (Richardson, 1981). Maximum current speeds are found across only a small span of the width of the current. Current speeds fall away gradually on either side of this region (Richardson *et al.*, 1969).

We believe it likely that most American eels cross the currents of the Gulf Stream system and enter Continental Slope Water as leptocephali. Leptocephali have been taken inshore of the Gulf Stream as far south as Cape Hatteras (Kleckner & McCleave, 1982) and were common in Slope Water collections north of Cape Hatteras from August through November. Metamorphosis to the glass eel phase

occurs inshore and offshore of the Gulf Stream system, however our limited data suggest that metamorphosing eels are rare on the offshore side. The absence of glass eels in collections taken in the Sargasso Sea adds credence to our belief that most eels traverse the Gulf Stream as leptocephali. Leptocephali of the European eel also undergo metamorphosis near the edge of the European continental slope (Schmidt, 1909a), presumably in water which is hydrographically distinct from mid-ocean water.

If American eel leptocephali are dependent on passive transport at this phase of their migration, a transport mechanism must exist to carry them from the oceanic to the continental side of the Gulf Stream. Similarities in the temperature-salinity characteristics of water masses below 500 m on either side of the Gulf Stream, led Stommel (1965) to suggest that deep-water cross-stream transfer may occur. This potential mechanism for cross-stream transport is probably not utilized by American eel leptocephali, inasmuch as their center of distribution in the current is above 350 m both night and day (Kleckner & McCleave, 1982).

As mentioned, the majority of American eel leptocephali enter the Florida Current along its seaward margin north of 30°N. At Cape Hatteras, less than 700 km downstream, leptocephali were distributed more evenly across the current (Kleckner & McCleave, 1982). We suggested that cyclic waves and eddies in the Florida Current may cause lateral mixing which would spread leptocephali across the current from east to west. Unfortunately, small scale patterns of flow within the Florida and Gulf Stream Currents, which might produce lateral mixing, have yet to be studied in detail. Randomly oriented lateral mixing would transport only a small part of the population from the oceanic to the continental side of the current, from which they could enter the Continental Slope Water. Many leptocephali would remain in the central flow of the current. These leptocephali would be carried rapidly to the east where they would enter one of the three branches of the Gulf Stream system southeast of the Newfoundland Rise. Obviously, if lateral mixing in the current has a westward bias, more leptocephali would be transported to the continental side of the current. Alternatively, if American eel leptocephali are capable of directed orientation and sustained swimming they might effect their own transport across the Gulf Stream system currents. In either case the number of leptocephali being transported out to the east, away from the continental land mass, would be reduced.

Detrainment of American eel leptocephali from the current across the Gulf Stream–Continental Slope Water front is a closely related problem. Passive mechanisms by which this might be accomplished may not exist. Stommel (1965) states that transfer across the current in the surface layers on a scale smaller than that of mesoscale eddies is not likely. This opinion is based on hydrographic data detailing a long, narrow band of cool, low salinity water on the west side of the current at depths of 0 m to about 120 m (Ford *et al.*, 1952). Stommel reasoned that, if small scale turbulent processes were active along the west side of the current, the integrity of this 1900 km long, 8 km wide filament of water could not be maintained.

Mesoscale Gulf Stream rings can effectively transport zooplankton between the

Sargasso Sea, the Gulf Stream and Continental Slope Water (Cox & Wiebe, 1979; Ring Group, 1981). However, we doubt that mesoscale eddy formation north of the Gulf Stream includes a sufficient volume to account for the transport of many American eel leptocephali from the current into Continental Slope Water. Approximately 5 to 8 warm core rings form inshore of the Gulf Stream in a year (Fuglister, 1972; Lai & Richardson, 1977). Richardson (1980) estimated the average exchange in the upper 150 m of water from the Gulf Stream to rings as $2 \times 10^6 \text{ m}^3 \text{ s}^{-1}$. If only warm core rings, north of the Gulf Stream are considered, this exchange represents less than 7% of the total estimated Gulf Stream transport in this layer (Richardson *et al.*, 1969). Furthermore, only rings formed while American eel leptocephali are abundant in the Gulf Stream would detrain significant numbers from the system. We can find no evidence in the oceanographic literature for a seasonal increase in warm core eddy formation. Unless as yet unidentified passive cross-stream transport mechanisms exist, we must assume that American eel leptocephali actively swim across and detrain from the currents of the Gulf Stream system.

This hypothesis is supported by the near absence of European eel leptocephali in our collections from the North American Continental Slope Water. Though not addressed specifically in our results, only three European eels were collected in North American Continental Slope Water (Figs 6 & 7) while many were taken in Gulf Stream system collections (Figs 3 to 8). If the leptocephali of both species are dependent on passive transport at this stage of their migration and if passive cross-stream transport mechanisms exist, it seems likely that many more European eel leptocephali would be found in North American Continental Slope Water collections.

Though Gulf Stream rings cannot significantly aid in the transport of numbers of American eel leptocephali, we believe that the region of the Gulf Stream east of the New England Seamounts, where the rings typically form, may be very important in their migration. Many leptocephali were taken here during August and September (Fig. 6). The reduction in current speed and increased path length created by large meanders and loops in the current may allow many American eels to actively move into Continental Slope Water before being carried east of the Southeast Newfoundland Rise.

We believe it likely that some eels carried east of Newfoundland may return to the southwest in the recirculation area south of the Gulf Stream (Richardson, 1981). Flow into this recirculation has been estimated as 60% to 100% of the total Gulf Stream transport (Mann, 1967; Worthington, 1976; Stommel *et al.*, 1978), while flow to the east across the Southeast Newfoundland Rise may be only intermittent (Fofonoff, 1981). The rate of transport in the recirculation area may be similar to the speed of cold core rings, which move to the southwest in the recirculation at about 5 cm s^{-1} (Richardson, 1980). This transport may allow some leptocephali to reenter and cross the Gulf Stream. The collection of American eel leptocephali thousands of kilometers from the coast during August through January (Figs 6, 7 & 8) indicates that a considerable number may fail to reach the coast, as concluded by Bruun (1963).

Knowledge of the continental distribution of the American eel is based on United States and Canadian government fishery statistics (Schmidt, 1909b; Vladykov, 1966; Fahay, 1978). These data are best considered to show only possible trends in the relative abundance of eels attaining a region of the coast, because fisheries are directed at older eels, the populations of which could have been altered by differential mortality. Furthermore, no estimate of fishing effort is included in these reports adding another potential bias to the data. With these caveats in mind, we can make the following regional listing of the relative number of eels moving inshore. The greatest concentrations probably occur in Quebec and the Canadian Maritime Provinces along the St. Lawrence estuary and also in the United States middle Atlantic region from New Jersey to Virginia. These regions are followed by the United States north Atlantic region from New York to Maine and more distantly by the southeastern Atlantic region from North Carolina to Florida. Comparatively few eels may attain the Gulf Coast region from Florida to Texas.

This distribution may be explained by our present understanding of North Atlantic Ocean, Gulf of Mexico and Caribbean Sea current systems and the utilization of these currents by migrating larval American eels. It is likely that eel abundance is low in the Gulf Coast region because comparatively few leptocephali enter the Gulf Stream system south of the Straits of Florida (Kleckner & McCleave, 1982). Eels in the Gulf Coast region must have been transported through passages in the Antilles Island arc, into the Caribbean, and finally through the Yucatan Channel into the Gulf of Mexico where they detrained from the Gulf Loop Current. Eel abundance in the southeastern Atlantic region may be higher than in the Gulf Coast region because of the influx of eels to the Florida Current north of the Straits of Florida. However, many eels are likely carried north of Cape Hatteras before they can cross to the continental side of the current. For this reason the greatest concentrations of American eels are found from north of Cape Hatteras to the Canadian Maritime Provinces and Quebec. Differences in apparent eel abundance within this range may be created by the westerly and southwesterly flow of the Continental Slope Water north of Cape Hatteras (Webster, 1969; Bumpus, 1973) and perhaps by the great reduction in the speed and increase in the path length of the Gulf Stream east of the New England Seamounts, which would allow many eels to detrain in this region.

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