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The northern limit of spawning by Atlantic eels (*Anguilla* spp.) in the Sargasso Sea in relation to thermal fronts and surface water masses

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ABSTRACT

American and European eels (*Anguilla rostrata* and *A. anguilla*) spawn in a large poorly defined area east of the Bahamas between about longitude 50W and 75W in the Sargasso Sea. We use the distribution of tiny *Anguilla* larvae taken in ichthyoplankton collections and associated characterizations of hydrography to test two hypotheses concerning distribution of water masses and the northern limit of spawning by both species. Data are presented from four transects of closely spaced stations conducted during February and April 1983 which refute our hypothesis that a positive correlation exists between the distribution of the Subtropical Underwater and spawning by *Anguilla*. Larvae ≤ 5.5 mm were taken on both sides of fronts at the northern edge of the Subtropical Underwater. This result was supported by data from two longer transects conducted during March 1985. Though Subtropical Underwater was not encountered along these transects tiny *Anguilla* larvae were present. Our second hypothesis, that fronts along the northern edge of the warm, saline surface water mass of the southern Sargasso Sea form the northern limit of spawning by *Anguilla*, was strongly supported by the March 1985 collections. Tiny *Anguilla* larvae were taken in all collections south of fronts separating southern Sargasso Sea surface water from mixed Subtropical Convergence Zone water to the north. *Anguilla* larvae ≤ 5.5 mm TL were not taken in collections at stations where mixed Subtropical Convergence zone water was present.

1. Introduction

Adult eels of the catadromous family Anguillidae from North America, *Anguilla rostrata*, and Europe, *A. anguilla*, leave inland and estuarine waters in the fall and migrate across hundreds to thousands of kilometers of open ocean to spawn in the Sargasso Sea during the late winter and spring. Adults have never been collected beyond the continental shelf. Thus, the pathways and orientation mechanisms utilized during the oceanic migration are unknown. What is known of the area and time of successful spawning has been inferred from the spatial and temporal distribution of

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tiny eel larvae³ identified in oceanographic collections. The seminal work in this regard was by Schmidt (1922 and 1935). Though challenged by Tucker (1959) and Vladikov and March (1975), the basic elements of Schmidt's hypotheses concerning the time and area of spawning have been supported in recent analyses of the available historical data by Boëtius and Harding (1985), Kleckner and McCleave (1982 and 1985) and McCleave *et al.* (1987) and by further ichthyoplankton surveys conducted by Schoth and Tesch (1982) and Wippelhauser *et al.* (1985). These descriptive studies form the base upon which we have begun to devise testable hypotheses concerning the mechanisms utilized by the Atlantic eels in attaining the spawning area. The work reported herein was designed specifically to test hypotheses concerning one of the hydrographic limits of the spawning area.

The first hypothesis was stated as follows by Kleckner *et al.* (1983; p. 291): ". . . thermal fronts separating the northern and southern surface water masses of the Sargasso Sea form the northern limit of American eel spawning. . . ." The hypothesis was based upon our observation that the smallest larvae in historical collections were taken in and south of the region of frontal activity in the subtropical convergence. This observation was supported by results from a West German survey cruise in 1979 (Schoth and Tesch, 1982; Wegner, 1982) and a preliminary study which we conducted along a thermal front in 1981 (Kleckner *et al.*, 1983). We believed that some feature of the surface water mass in the southern Sargasso Sea serves as a cue for adult eels to cease migrating and begin spawning activity. The second hypothesis, which remained 'in press' for an extended period, was stated as follows by Kleckner and McCleave (1985; p. 67): "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." The hypothesis was based upon our observation that the European eel spawning area, as defined by Schmidt (1935), lies in the region of Subtropical Underwater formation (Worthington, 1976) and that this shallow, warm, salinity maximum water frequently penetrates far to the west (Gunn and Watts, 1982) into the American eel spawning area.

In the following sections we present the results of six transects of trawl and hydrographic stations which were conducted specifically to test these hypotheses. The results allow our acceptance of the first hypothesis, that fronts separating the northern and southern surface water masses in the Sargasso Sea form the northern limit of successful spawning by American and European eels, and rejection of the second hypothesis, that a positive correlation exists between the spatial distribution of spawning and the Subtropical Underwater.

2. Sampling rationale

Here, we have used the distribution of small *Anguilla* larvae taken in zooplankton collections in the Sargasso Sea to identify those water masses in which spawning had

3. Throughout the manuscript the general terms larva and larvae are used instead of leptocephalus and leptocephali, the specific singular and plural terms for larval eels.

and had not recently occurred. This procedure will give a reasonable estimate of the distribution of successful spawning when the time between fertilization and capture is brief relative to either the rate at which currents advect larvae from the spawning area or to the rate at which turbulent mixing alters the characteristics of the water mass in which spawning occurred.

In the following sections we have focused our analyses on the distribution of *A. rostrata* and *A. anguilla* larvae ≤ 7.5 mm in total length. Such larvae were likely spawned within the preceding three weeks. Embryonic durations of 35 to 60 h have been determined in laboratory studies of embryogenesis in the European eel and the closely related Japanese eel, *A. japonica* (Yamamoto and Yamauchi, 1974; Research Group on Eel Reproduction, 1978; Bezdenezhnykh *et al.*, 1983). The larvae hatched as primitive prelarvae 2.9 to 3.5 mm long; they retained a portion of the embryonic yolk sac and oil droplet, the mouth and anus had not yet opened, and retinal pigment, teeth and pectoral fins were lacking (Yamamoto *et al.*, 1975). All larvae found in the collections we made had teeth, pectoral fins and pigmented retinae—structures which develop in laboratory-reared *A. japonica* prelarvae from the third through the eleventh day after hatching (Yamauchi *et al.*, 1976). By the fourteenth day *A. japonica* had attained a length of 7.0 to 7.6 mm (Yamauchi *et al.*, 1976; Research Group on Eel Reproduction, 1978). Thus, under laboratory conditions at 19° to 24.5°C, embryogenesis and early larval development in the Anguillidae are rapid. Water temperature in the spawning area, which influences developmental rate, is no lower at depths between 50 m and 300 m where tiny *Anguilla* larvae are found (Castonguay and McCleave, 1987).

Historically, the mean circulation in the western North Atlantic subtropical gyre was believed to include a persistent Antilles Current flowing to the northwest along the outer Antilles/Bahamas arc to merge with the Gulf Stream, while toward the center of the gyre flow was greatly reduced (Wüst, 1924; Iselin, 1936). Recent studies have shown that currents along the island arc are neither persistent (Gunn and Watts, 1982) nor continuous (Olson *et al.*, 1984).

To the north in the area of the subtropical convergence between approximately 22N and 32N flow is dominated by closely packed cyclonic and anticyclonic mesoscale eddies with average diameters of 200 km and speeds around the periphery of 20 km day⁻¹ (Voorhis *et al.*, 1976). The eddies distort the mean meridional surface temperature gradient by advecting northern and southern water masses to form meridionally oriented warm and cold plumes with widths of 40 to 50 km and north-south extents of about 200 km (Voorhis *et al.*, 1976). These features form and dissipate on a time scale of several months. At the eddy peripheries small scale baroclinic disturbances generate cold cyclones and warm anticyclones in the upper 100 to 200 m (Voorhis and Bruce, 1982). These features move with the mesoscale surface currents at speeds on the order of 20 km day⁻¹ and may form and dissipate on a time scale of several days. Areas of small scale front formation occur between the opposing water masses as water converging on their boundaries is advected away to the east in

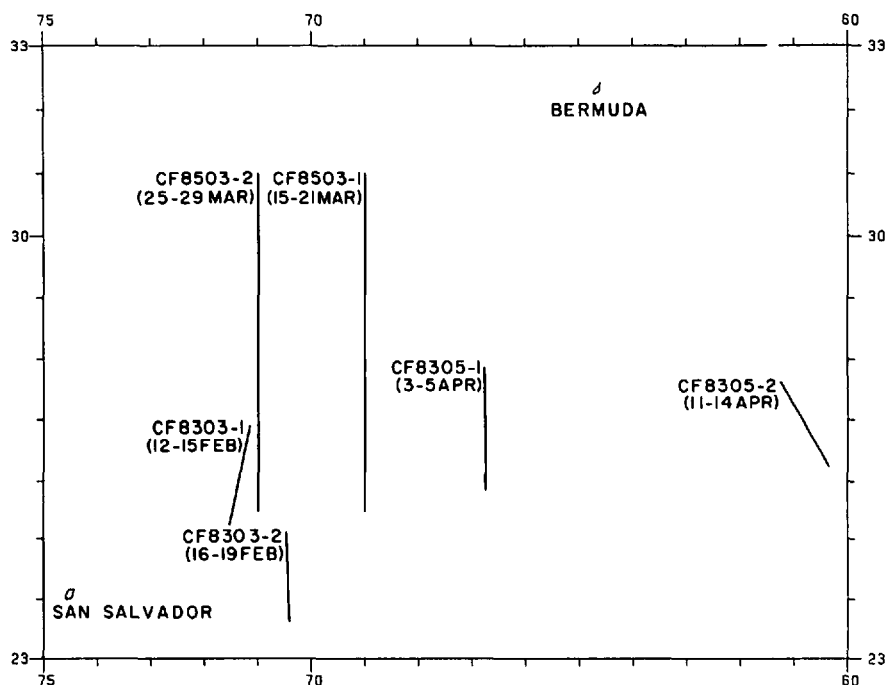


Figure 1. Locations and dates for CF8303, CF8305 and CF8503 transects. Station positions along the transects are shown on Figures 2, 3, 8 and 9.

accelerating frontal jets which attain speeds of 50 to 100 cm sec⁻¹ over widths of <10 km and depths of <50 m (Katz, 1969; Voorhis and Bruce, 1982). Experiments with "window shade" drogues set at different depths indicate that the speed of the frontal jets decreases rapidly at depths below 50 m (Voorhis and Bruce, 1982). Thus, *Anguilla* larvae, which inhabit depths between 50 m and 300 m (Castonguay and McCleave, 1987), are below the greatest influence of these currents. However, advective transport generated by the deeper surface currents associated with mesoscale features is sufficient to move two or three week old larval eels tens if not hundreds of kilometers from the areas where they were spawned.

For this reason, the validity of our experimental technique was dependent on the identification of the likely origin of the water masses in which our collections were taken. Though mixing occurs between the surface layers of the subtropical convergence, we believed it to be sufficiently limited during the late winter and early spring, when the greatest density gradients exist between the northern and southern water masses, to permit such analysis on a broad scale of tens of kilometers.

3. Data and methods

Data for this study were collected along transects made during cruises of the ORV Cape Florida in 1983 (CF8303 and CF8305) and 1985 (CF8503) (Fig. 1). CF8303

transects were scheduled and positioned to be in the American eel spawning area at the predicted time of peak spawning based on data available to us at that time (Kleckner and McCleave, 1985). CF8305 was scheduled during the predicted time of peak spawning of the European eel; transect 1 was positioned well west of the center and transect 2 near the center of the European eel spawning area. Because of low catches during CF8303, CF8503 was scheduled later in the American eel spawning season.

Transects during the two years differ in a number of respects. In 1983 an attempt was made to center the transects perpendicularly across sharp frontal features identified initially by means of data from infrared satellite imagery. Final positioning was based on continuous records of temperature at 3 m deep and casts of expendable bathythermographs (XBT) made immediately preceding each transect. The station distribution along the transects was nonuniform. A station was positioned near the center of the surface expression of each front and at distances of approximately 9, 18, 37, and 74 km on either side of the region of rapid change in surface temperature. Variation in the width of fronts, changes in the position of fronts during the north and south legs of a transect, and inaccuracy of navigation led to variation in this pattern. Transects were sampled in one leg from north to south across the fronts during CF8303. Transects were sampled in two legs during CF8305, first to the north from the front (stations 4 to 1) and then to the south from the front (stations 5 to 9). (Transect stations were numbered consecutively from north to south for all cruises.)

The two 1985 transects, each 611 km long, were positioned latitudinally to span the area of maximal frontal activity in the subtropical convergence. This area was identified from analyses of historical high-resolution, infrared imagery and a pair of XBT transects made in February 1985 (P. Cornillon, personal communication). The transects were positioned longitudinally to pass near the center of the American eel spawning area (Kleckner and McCleave, 1985; Wippelhauser *et al.*, 1985). Stations were located at 56-km intervals along the transects; they were sampled from north to south on the first transect and from south to north on the second transect.

Larvae were sampled at each station with a 3-m Isaacs Kidd Midwater Trawl with a mouth area of 8.68 m² and a filtering area of 68.9 m² (Table 1). The trawl was fully lined with 0.505 mm NITEX netting and had a filtering area ratio (Smith *et al.*, 1968) of 4:1. The depth of the net was relayed in real time from a pressure-sensitive ultrasonic transmitter (Communication Associates Inc., model CDS) to a trailing hydrophone (CAI model CN-15 or CS-40). The pulsed signal was received, translated and displayed as depth (CAI model CR-40 receiver and model CI-40 decoder). The system functioned poorly on the 1983 cruises due to noise. Transfer of the hydrophone conductor winch from the stern to amidships and deployment of the hydrophone over the side amidships on the 1985 cruise removed the acoustical-electrical interference. A permanent record of fishing depth was provided by a mechanical time-depth recorder (Benthos Inc.).

At each station one (1983) or two (1985) oblique tows of the Isaacs Kidd Midwater Trawl were made to a nominal depth of 300 m (Table 1). Variation in the pattern

Table 1. Patterns of sampling tows for eel larvae by cruise and transect.

Cruise number	Transect number	Tows per station	Deployments per tow	Winch speed (cm sec ⁻¹) deploy, retrieve
CF8303	1	1	1	17, 17
CF8303	2	1	1	17, 17
CF8305	1	1	2	34, 17
CF8305	2	1	2	34, 17
CF8503	1	2	1	17, 17
CF8503	2	2	1	17, 17

Cruise number	Transect number	Maximum tow depth (m)			Tow duration (min)		
		mean	SE	min.-max.	mean	SE	min-max.
CF8303	1	326	15.5	250-400	122	4.4	86-138
CF8303	2	289	16.6	187-380	120	4.5	91-141
CF8305	1	286	16.0	250-395	158	6.2	118-174
CR8305	2	257	1.9	248-266	158	5.9	129-179
CF8503	1	300	0.6	298-306	242	12.0	140-300
CF8503	2	301	0.8	299-312	241	6.2	184-274

Cruise number	Transect number	Water filtered (10 ⁴ m ³)			Tow speed (cm sec ⁻¹)		
		mean	SE	min.-max.	mean	SE	min-max.
CF8303	1	5.9	0.30	4.5-7.7	93	5.1	74-124
CF8303	2	5.3	0.50	2.7-8.5	85	6.2	57-132
CF8305	1	6.0	0.59	3.4-8.4	73	5.8	37-94
CF8305	2	6.5	0.41	4.1-7.9	78	2.9	62-92
CF8503	1	10.6	0.98	6.2-16.6	83	4.8	48-106
CF8503	2	11.2	0.51	6.7-14.1	88	2.1	70-98

All tows were oblique; that is, they were deployed to their maximum depth and retrieved immediately. Tows deployed multiply were retrieved to a depth of 10 m and redeployed. Winch speeds are the nominal rates at which wire was spooled off or onto the drum.

Water filtered was estimated from counts recorded by a flow meter (Rigosha model 2536) suspended at the center of the trawl mouth: water filtered (m³) = count (rev) · calibration factor (m rev⁻¹) · trawl mouth area (m²).

Tow speed was estimated as follows: tow speed (cm sec⁻¹) = [count (rev) · calibration factor (m rev⁻¹)] / tow duration (sec).

occurred due both to our decision process and to factors beyond our control, such as malfunctioning of equipment and water currents.

Samples were fixed and preserved in 7.5% formalin-seawater. Eel larvae were sorted from the samples using a dissecting microscope. *Anguilla* larvae were identified following Kleckner *et al.* (1983) and Kleckner and McCleave (1985). Only specimens identifiable to species are included in the analysis. Total length (TL) of each specimen was measured to the nearest 0.1 mm.

Catch per unit effort in terms of larvae per 10⁴ m³ of water filtered was computed for each species and tow. For the 1985 cruise in which there were two tows per station, no

significant difference was found in the catch per unit effort of either species between the tows taken first and the tows taken second at each station (paired *t*-tests, $p > 0.05$). Also the mean lengths of larvae of either species taken in the first and second tows at the stations along the transects in 1985 were not significantly different (*t'* tests of equality of means of two samples, assuming unequal variances, $p > 0.05$; Sokal and Rohlf, 1981). Therefore, the number of larvae and amount of water filtered in paired tows were combined for analysis.

Conductivity-temperature-depth (CTD) profiles, taken with several different configurations of the Neill Brown CTD, were calibrated by standard techniques against water samples collected during each profile. CTD profiles were taken at all stations with the following exceptions: the northern station (station 1) of CF8303 transect 1 and of CF8305 transects 1 and 2. Estimates of density (σ_t) were calculated for these stations based on their XBT profiles and the temperature-salinity correlations of adjacent stations. On CF8503 XBT profiles were taken half way between stations and following the second tow of a station pair.

4. Water mass types

Successful tests of the two hypotheses depend upon the ability to identify surface layer water masses in the central Sargasso Sea. These include 18°C Water, northern Sargasso Sea surface water, southern Sargasso Sea surface water, mixed convergence zone surface water and Subtropical Underwater.

The 18°C Water (Worthington, 1959), also called Subtropical Mode Water (Masuzawa, 1969; Gunn and Watts, 1982), forms the deepest layer. It may be recognized by its characteristic temperature ($17.9^\circ \pm 0.3^\circ\text{C}$) and salinity ($36.5\text{‰} \pm 0.1\text{‰}$) correlation (Worthington, 1959), though for convenience it is frequently defined to include the 17° to 19°C temperature range. During the winter convective overturn north of Bermuda, 18°C Water may extend from the surface to the top of the main thermocline. The 18°C Water spreads out across this density barrier penetrating beneath the warmer surface layers to the south. North of 32N the 18°C Water layer is always greater than 250 m thick; to the south it narrows, becoming vertically indistinct at approximately 22N as the permanent tropical thermocline merges with the main thermocline (Worthington, 1959; Wegner, 1982). Here and to the south, a narrow layer of water with the temperature-salinity correlation of 18°C Water is still present at about 300 m (Worthington, 1976).

The temperature and salinity characteristics of northern Sargasso Sea surface water during the winter and early spring are similar to those of 18°C Water. Due to downwelling, associated with the formation of the 18°C Water, the surface water never cools below 17°C in the northern Sargasso Sea (Worthington, 1959). As spring progresses the northern surface water warms and becomes increasingly stratified as the seasonal thermocline forms above the 18°C Water (Leetmaa, 1977). The salinity of

this water mass is usually less than 36.6‰, though salinities as high as 36.7‰ have been recorded in the northern surface water mass (Elrod and Kester, 1985).

Relative to northern surface water, southern Sargasso Sea surface water is warm, saline and permanently stratified (Worthington, 1976). However, despite recent interest in the patterns of circulation in the southwestern Sargasso Sea (Gunn and Watts, 1982; Olson *et al.*, 1984), the temperature and salinity characteristics of the southern surface water mass have not been clearly defined. Two studies do give an indication of its characteristics. The temperature-salinity plot of western Sargasso Sea stations south of 27N during April shown by Wegner (1982; Fig. 7) and the plot of data collected during May south of a strong thermal front near 30N, 70W shown by Katz (1969; Fig. 8) have similar patterns of correlation. Water in the upper 125 m had maximum temperatures above 21.5°C and a wide range of salinities between 36.55‰ and 37.2‰. In the subtropical convergence zone, surface waters of the northern and southern Sargasso Sea mix forming a water type with intermediate characteristics (Katz, 1969; Wegner, 1982). Because temperatures and salinities in the mixed water overlap those of the adjacent water masses, identification of the mixed water by means of T-S diagram analysis is frequently impossible. In his discussion of layering in the subtropical convergence, Wegner (1982) used density to differentiate these water masses. Northern Sargasso Sea surface water and 18°C Water were characterized as having densities greater than σ_t 26.2. This equates to a temperature-salinity correlation of approximately 18.2°C and 36.6‰. Southern Sargasso Sea surface water was characterized as having a density less than σ_t 25.6. This equates to a temperature-salinity correlation of approximately 21.5°C and 36.6‰. Densities between σ_t 25.6 and 26.2 were characterized as being associated with mixed convergence zone water. These conventions are used in the following sections.

The variable high salinities found in the southern Sargasso Sea surface water mass are caused by variation in the production and penetration into the region of Subtropical Underwater. The Subtropical Underwater is identified as a subsurface salinity maximum layer ($\geq 36.7‰$) occurring at depths between 50 and 200 m (Worthington, 1976; Gunn and Watts, 1982; Olson *et al.*, 1984). It is produced by the convergence of saline water in an area of high evaporation under the trade winds in the south central subtropical gyre (Worthington, 1976). Changes in precipitation and evaporation can cause variation in the production of this water mass. Also, because the surface mixed layer may penetrate below 100 m during January and February, the top part of the Subtropical Underwater is exposed to dilution during the winter (Olson *et al.*, 1984).

5. CF8303 and CF8305 hydrography

The front surveyed during CF8303-1 sloped downward from its surface expression at station 5 to a depth of 200 m at station 9 (Fig. 2A, B, C). Southern surface water, found in the upper 100 m on both sides of the front, was 1° to 2°C warmer to the south. It was relatively fresh ($< 36.6‰$) with the exception of two saline pockets of water in

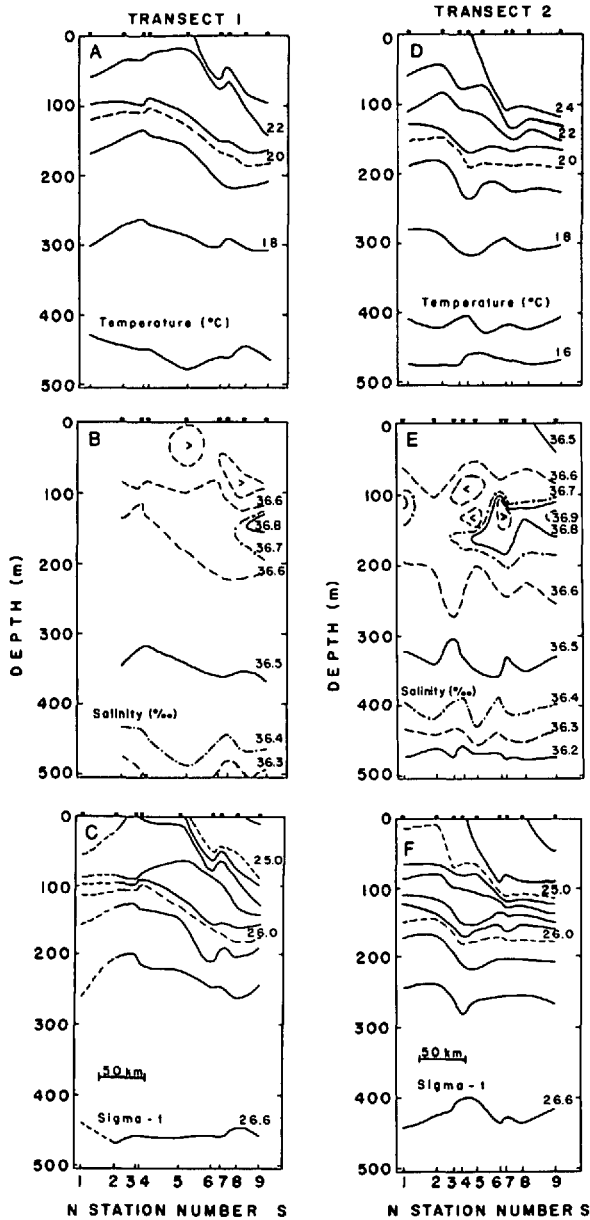


Figure 2. Temperature (A & D), salinity (B & E) and density (C & F) profiles along CF8303 transects 1 and 2. Relative station positions along the transects are indicated by tick marks at the bottom of each figure. Tick marks along the top of temperature and density figures indicate position of CTD or XBT profiles; those along the top of salinity figures indicate position of CTD profiles. Sigma-*t* values at transect 1 station 1 are estimates derived from the XBT temperature profile and station 2 CTD temperature-salinity correlations.

and south of the front. Beneath the surface layer the isopycnals of 25.6 and 26.2 σ_t used to delimit mixed convergence zone water closely followed the upper and lower 36.6‰ isohalines at stations 1 to 7. This saline layer doubled in thickness in the area of the front and then merged with high salinity Subtropical Underwater between 100 m and 200 m at stations 8 and 9. The 18°C Water mass thinned about 50 m to the south beneath the slope of the front.

Surface expression of the front surveyed during CF8303-2 was centered on station 3 (Fig. 2D, E, F). Subsurface expression of the front extended vertically to 250 m and horizontally to station 7. Southern surface water, found on both sides of the front, was relatively warm ($>22^\circ\text{C}$) and fresh ($<36.6\text{‰}$). Unlike CF8303-1, the layer between the upper and lower 36.6‰ isohalines included high salinity Subtropical Underwater on both sides of the front. The layer of 18°C Water thinned only slightly to the south beneath the front.

Surface expression of the front surveyed during CF8305-1 was centered between stations 4 and 5 (Fig. 3A, B, C). Subsurface expression of the front, as shown by increased isopleth depths, extended vertically to at least 500 m and horizontally to station 8. North of the front a 50 m to 60 m layer of relatively cool ($\leq 22^\circ\text{C}$), low salinity ($<36.6\text{‰}$) southern surface water overlay mixed convergence zone water. South of the front a 100 m layer of warm ($>24^\circ\text{C}$) low salinity southern surface water overlay high salinity Subtropical Underwater centered at about 175 m. A 200 m thick layer of 18°C Water north of the front was displaced downward by 100 m to the south.

The front surveyed during CF8305-2 sloped downward sharply from its surface expression between stations 4 and 5 to 200 m at station 6 (Fig. 3D, E, F). Southern surface water, found on both sides of the front, was saline ($>36.6\text{‰}$) with the exception of a small pocket of 36.5‰ water in the upper 50 m at stations 4 and 5. At stations 1 and 2 a 50 m layer of relatively cool ($<22^\circ\text{C}$) southern surface water overlay mixed convergence zone water. South of the front a 120 m layer of warm ($>22^\circ\text{C}$) southern surface water, which included salinities greater than 37‰, overlay Subtropical Underwater centered at 160 m. A 200 m thick layer of 18°C Water north of the front was displaced downward by 50 m south of the front.

6. Distribution of *Anguilla* larvae during CF8303 and CF8305

The fronts surveyed during CF8303-1, CF8305-1 and CF8305-2 separated subsurface layers of mixed convergence zone water to the north from Subtropical Underwater to the south with southern surface water present on both sides (Table 2, Figs. 4, 5, 6, 7). If Subtropical Underwater contains a cue which triggers the cessation of migration and the initiation of spawning by adult American or European eels, it follows that, to the extent that mixing is restricted across a front, the distribution of recently hatched larvae would be restricted to waters south of the front. This was not the case. American and European eel larvae ≤ 7.5 mm TL were taken in collections on both sides

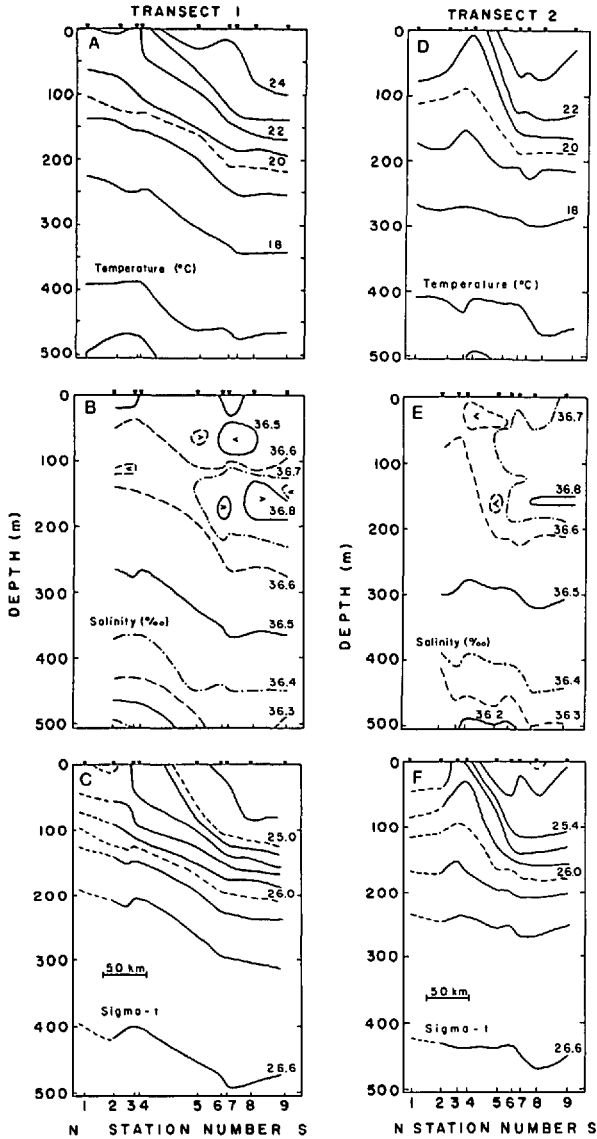


Figure 3. Temperature (A & D), salinity (B & E) and density (C & F) profiles along CF8305 transects 1 and 2. Relative station positions along the transects are indicated by tick marks at the bottom of each figure. Tick marks along the top of temperature and density figures indicate position of CTD or XBT profiles; those along the top of salinity figures indicate position of CTD profiles. Sigma- t values at the first station of transects 1 and 2 are estimates derived from their XBT temperature profiles and respective station 2 CTD temperature-salinity correlations.

Table 2. Occurrence (+) of American and European eel larvae ≤ 7.5 mm TL and water mass types at CF8302, CF8305 and CF8503 stations.

Cruise-transect	Station number								
	1	2	3	4	5	6	7	8	9
CF8303-1									
American eel			+						+
European eel									
SSSW	+	+	+	+	+	+	+	+	+
MCZW	+	+	+	+	+	+	+	+	+
SUW							+	+	+
18W	+	+	+	+	+	+	+	+	+
CF8303-2									
American eel		+	+	+	+	+	+	+	+
European eel									
SSSW	+	+	+	+	+	+	+	+	+
MCZW	+	+	+	+					
SUW	+			+	+	+	+	+	+
18W	+	+	+	+	+	+	+	+	+
CF8305-1									
American eel	+	+		+	+	+	+	+	
European eel	+	+	+	+	+	+	+	+	+
SSSW	+	+	+	+	+	+	+	+	+
MCZW	+	+	+	+					
SUW					+	+	+	+	+
18W	+	+	+	+	+	+	+	+	+
CF8305-2									
American eel									
European eel	+	+	+			+	+	+	+
SSSW	+	+	+	+	+	+	+	+	+
MCZW	+	+	+	+					
SUW					+	+	+	+	+
18W	+	+	+	+	+	+	+	+	+

of the fronts sampled during the four transects in 1983 (Table 2). These included very small larvae ≤ 5.5 mm TL taken at CF8305-1 stations 2, 3, and 4 (Fig. 6B) and CF8305-2 station 1 (Fig. 7B), stations at which the salinity maximum layer of the Subtropical Underwater was not present (Fig. 3B, E).

Though the relative abundance of all American eel larvae taken in the April CF8305-1 collections (Fig. 6A) was an order of magnitude greater than in the February CF8303-2 collections (Fig. 5A), the relative abundance of recently hatched larvae (≤ 7.5 mm TL) was remarkably similar. Calculated as total number of American eel larvae ≤ 7.5 mm TL divided by total volume of water filtered during positive tows, CF8303-2 and CF8305-1 had catch rates of 0.35 and 0.33 specimens per

Table 2. (Continued)

	Station number											
CF8503-1	1	2	3	4	5	6	7	8	9	10	11	12
American eel							+		+	+	+	+
European eel						+	+		+	+		+
SSSW						+	+	+	+	+	+	+
MCZW		+	+	+	+	+	+	+	+	+	+	+
SUW												
18W	+	+	+	+	+	+	+	+	+	+	+	+
CF8503-2	1	2	3	4	5	6	7	8	9	10	11	12
American eel										+	+	+
European eel												+
SSSW							+			+	+	+
MCZW	+	+	+	+	+	+	+	+	+	+	+	+
SUW												
18W	+	+	+	+	+	+	+	+	+	+	+	+

SSSW = southern Sargasso surface water, SUW = subtropical underwater, MCZW = mixed convergence zone water and 18W = eighteen degree water.

10⁴ m³, respectively. This was an unexpected result because, though both transects were well within the spatial limits of the American eel spawning area (McCleave and Kleckner, 1985) the peak time of spawning of the American eel was believed to be during February (Schmidt, 1922; Kleckner and McCleave, 1985). That American eels had been spawning for an extended period can also be seen in the size range of 4.2 to 27.2 mm TL taken along CF8305-1. The four American eel larvae taken during CF8305-2 (Fig. 7B) were all large (13.9 to 18.1 mm TL). This transect (Fig. 1) was probably near the eastern limit of known American eel spawning (Schoth and Tesch, 1982; Wippelhauser *et al.*, 1985; McCleave *et al.*, 1987).

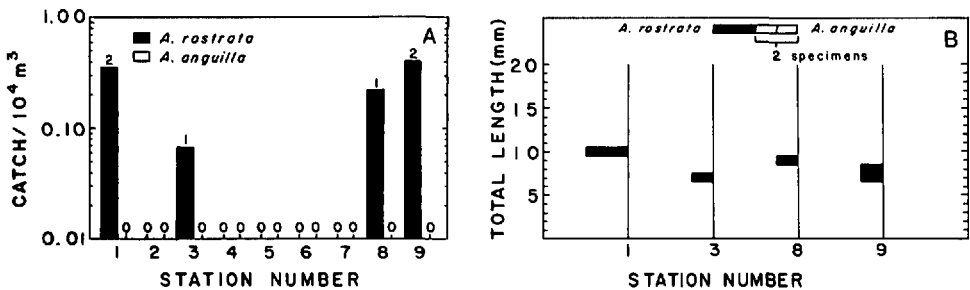


Figure 4. Cruise CF8303 transect 1. (A) Catch as larvae of all sizes, expressed as number of larvae per 10⁴ m³ of water filtered, of American eel (*Anguilla rostrata*) at each station. The number of larvae taken is listed above each bar. (B) Total lengths of American eel larvae at each station along the transect.

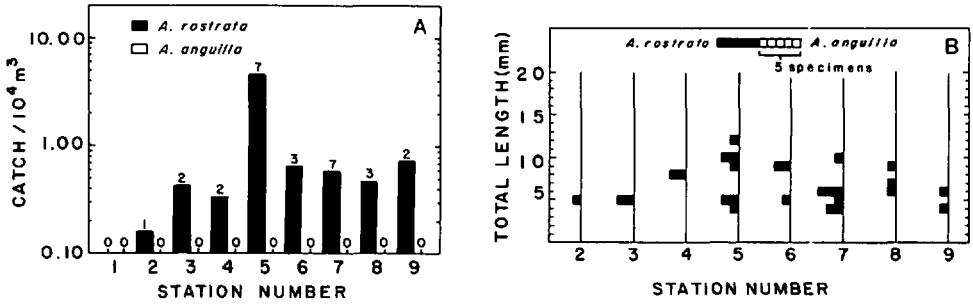


Figure 5. Cruise CF8303 transect 2. (A) Catch as larvae of all sizes, expressed as number of larvae per 10^4 m^3 of water filtered, of American eel and European eel (*A. anguilla*) at each station. The number of larvae taken is listed above each bar. (B) Length-frequencies of American and European eel larvae at each station along the transect.

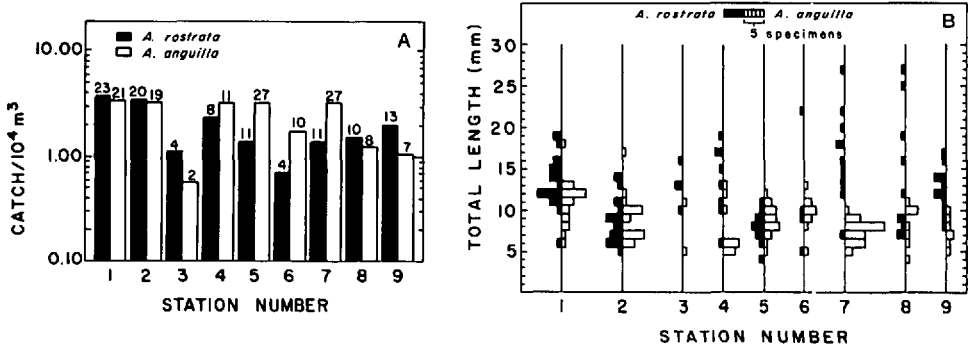


Figure 6. Cruise CF8305 transect 1. (A) Catch as larvae of all sizes, expressed as number of larvae per 10^4 m^3 of water filtered, of American eel and European eel at each station. The number of larvae taken is listed above each bar. (B) Length-frequencies of American and European eel larvae at each station along the transect.

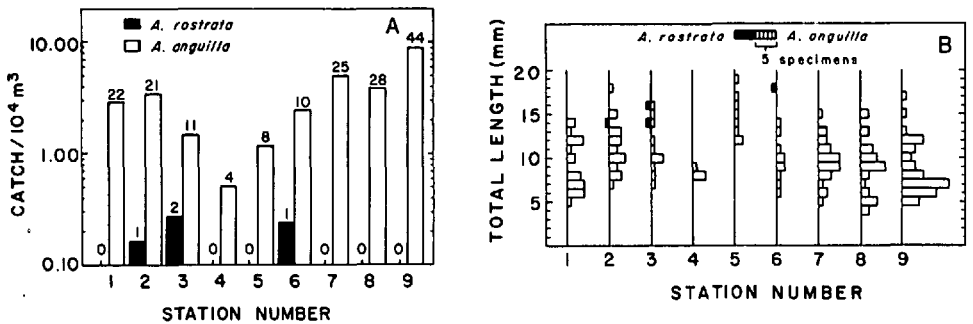


Figure 7. Cruise CF8305 transect 2. (A) Catch as larvae of all sizes, expressed as number of larvae per 10^4 m^3 of water filtered, of American eel and European eel at each station. The number of larvae taken is listed above each bar. (B) Length-frequencies of American and European eel larvae at each station along the transect.

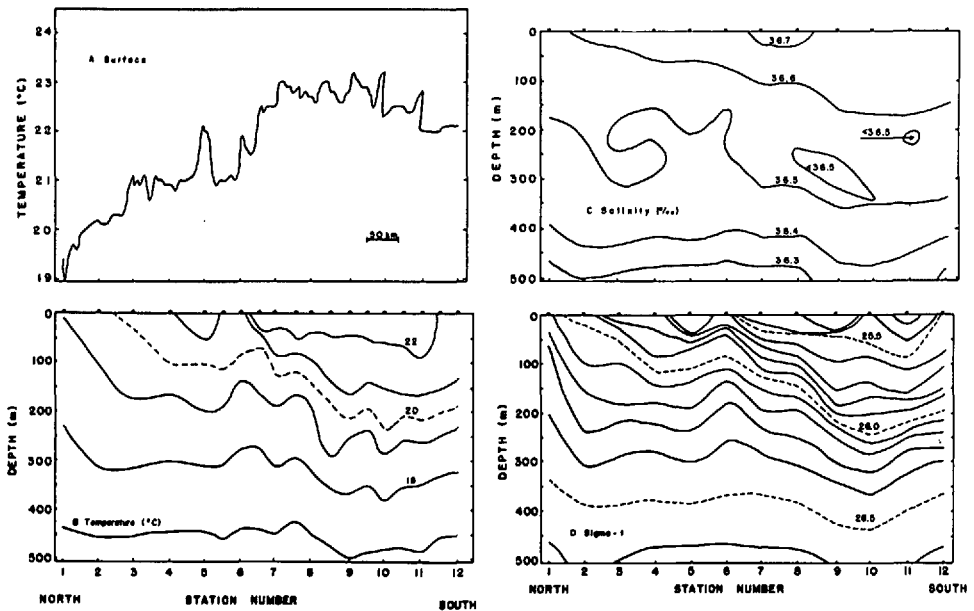


Figure 8. (A) Surface temperature and (B) subsurface temperature, (C) salinity and (D) density profiles along CF8503 transect 1. Relative station position along the transect is indicated by tick marks at the bottom of each figure. Tick marks along the top of the subsurface temperature figure indicate the position of CTD or XBT profiles; those along the top of the salinity and density figures indicate the position of CTD profiles.

No European eel larvae were taken during CF8303. The relative abundance of all European eel larvae taken in collections along CF8305 transects 1 and 2 was similar (Figs. 6A and 7A). Catch rates for recently hatched larvae (≤ 7.5 mm TL) were 0.80 and 0.84 specimens per 10^4 m³, respectively. This too is a surprising result because CF8305 transect 1 was positioned at what we thought was rather far west in the European eel spawning area while transect 2, some 500 km east of transect 1, was located more centrally in the spawning area (McCleave and Kleckner, 1985).

7. CF8503 hydrography

Surface thermal gradients of $> 1.0^\circ\text{C}$ in < 20 km between CF8503-1 stations 1 and 2 and stations 6 and 7 (Fig. 8A) formed the northern limits of two separate fronts. Subsurface expression of the northern front, as shown by increased isopleth depths, extended vertically to at least 400 m and horizontally to station 2 (Fig. 8B, C, D). At station 1 the patterns of temperature and salinity distribution and the density index approached values characteristic of northern surface water. The weakly stratified surface water mass south of the northern front had the density range of $\sigma\text{-}t$ 25.6 to 26.2, characteristic of mixed convergence zone water. The mixed water penetrated to about 175 m and was underlain by a 225 m thick layer of 18°C Water as indicated by

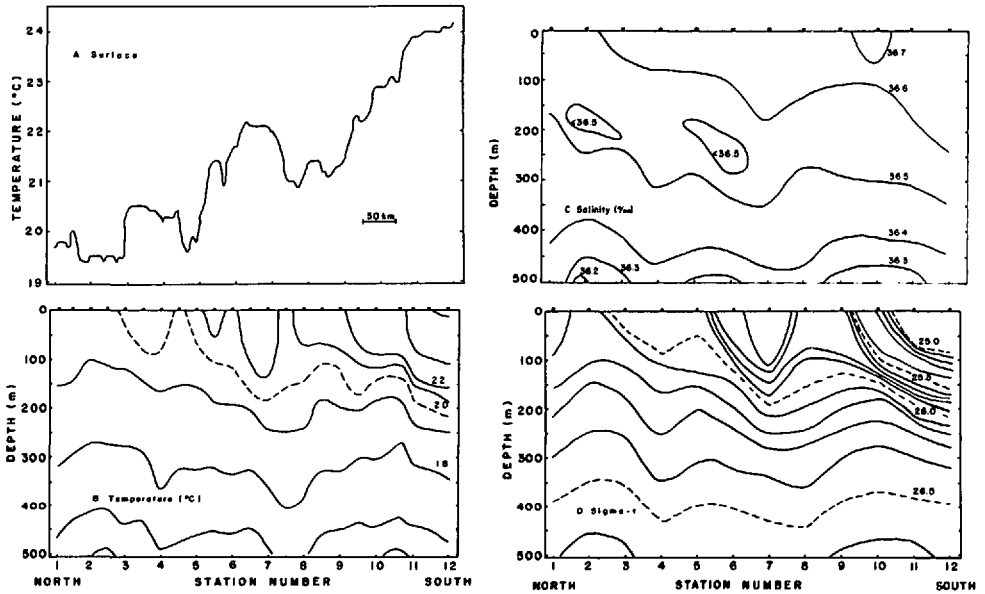


Figure 9. (A) Surface temperature and (B) subsurface temperature, (C) salinity and (D) density profiles along CF8503 transect 2. Relative station position along the transect is indicated by tick marks at the bottom of each figure. Tick marks along the top of the subsurface temperature figure indicate the position of CTD or XBT profiles; those along the top of the salinity and density figures indicate positions of CTD profiles.

the depth of the 36.4‰ isohaline. Subsurface expression of the southern front beginning at station 6 extended vertically to 500 m and horizontally to between stations 8 and 9. The front formed the northern border of a 110 m pool of warm ($>21.5^{\circ}\text{C}$) saline ($>36.6\text{‰}$) southern surface water. Below, mixed convergence zone water formed a highly stratified 150 m to 200 m thick layer atop the 18°C Water. The 18°C Water mass thinned by 130 m beneath the southern front. A reduction in salinity of 0.02 to 0.05‰ occurred at the top of the 18°C Water at all stations except station 1. In Figure 8C this salinity drop appears as pockets of anomalously fresh water at stations 4 to 6 and 8 to 10. Subtropical Underwater was not found along this transect.

Surface temperatures between stations 1 and 9 on CF8503-2 showed alternating bands of warm and cold water (Fig. 9A) embedded in the general pattern of increasing temperature and salinity and decreasing density to the south (Fig. 9B, C, D). These bands resembled the alternating tongues of warm and cold surface water previously noted in the subtropical convergence by Voorhis and Bruce (1982). The bands were separated by sharp frontal boundaries and appeared to affect isopleths to depths of at least 500 m. They lay in an area of mixed convergence zone surface water similar to that in the surface layer between CF8503-1 stations 2 to 6 (Fig. 8). A 100 m deep pool of warm water with the density index of southern surface water (<25.6 sigma- t) was centered on station 7. A series of step like surface thermal fronts between stations 9 and

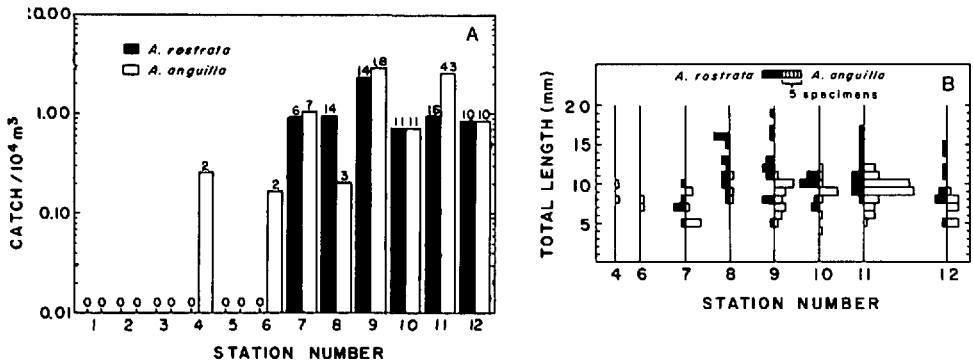


Figure 10. Cruise CF8503 transect 1. (A) Catch as larvae of all sizes, expressed as number of larvae per 10^4 m³ of water filtered, of American eel and European eel at each station. The number of larvae taken is listed above each bar. (B) Length-frequencies of American and European eel larvae at each station along the transect.

11 (Fig. 9A) lay at the northern edge of a 150 m deep layer of warm saline southern surface water (Fig. 9B, C, D). South of the front mixed convergence zone water was reduced to a highly stratified 75 m thick layer between the southern surface water and the underlying 18°C Water mass at 200 m to 250 m. The 18°C Water thinned by 100 m south of the front. A reduction in salinity of 0.01 to 0.02‰ was found at the top of the 18°C Water at all stations along the transect. In Figure 9C this salinity drop appears as pockets of anomalously fresh water at stations 2, 3, 5, and 6. Subtropical Underwater was not found along this transect.

8. Distribution of *Anguilla* larvae during CF8503

Fronts found to the south along CF8503 transects 1 and 2 separated deep pools of warm saline southern surface water from mixed convergence zone water to the north. If southern surface water contains a cue which triggers the cessation of migration and the initiation of spawning by adult American or European eels, it follows that, to the extent that mixing is restricted between the two water masses, the distribution of recently hatched larvae would be restricted to waters south of the fronts. This was the case. The northern limit of specimens ≤ 7.5 mm TL along transect 1 was between stations 5 and 6 for European eel larvae and stations 6 and 7 for American eel larvae (Table 2). Along transect 2, this limit was between stations 9 and 10 for American eel larvae. Too few European eel larvae were taken along transect 2 for such a determination (Fig. 11B). These limits coincided with the fronts at the northern borders of the southern surface water (Table 2). All larvae ≤ 5.5 mm TL were taken at stations where southern surface water was present. Larvae were not found in collections at CF8503-1 station 5 (Fig. 10B) or CF8503-2 station 7 (Fig. 11B). These stations included pools of southern surface water, which may have been isolated from the main body of southern surface water to the south. Collections of larger American

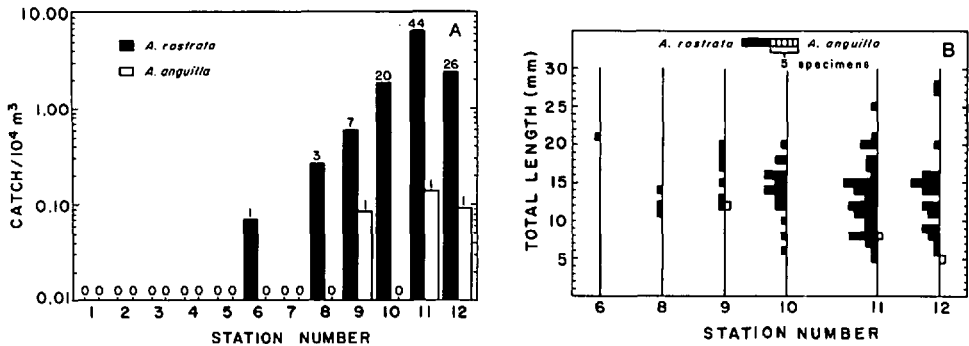


Figure 11. Cruise CF8503 transect 2. (A) Catch as larvae of all sizes, expressed as number of larvae per 10^4 m³ of water filtered, of American eel and European eel at each station. The number of larvae taken is listed above each bar. (B) Length-frequencies of American and European eel larvae at each station along the transect.

and European eel larvae taken north of the southern surface water fronts included relatively few specimens (Fig. 10B; station 4 and Fig. 11B; stations 6, 8, 9).

The CF8503 transects were positioned near the center of the American eel spawning area and west of the center of European eel spawning. This was reflected in the relative abundance of their larvae in these collections. European eel larvae were an order of magnitude more abundant in CF8503-1 collections (Fig. 10A) than they were to the west in CF8503-2 collections (Fig. 11A). The combined catch rate for recently hatched European eel larvae ≤ 7.5 mm TL in CF8503-1 collections taken south of the southern surface water front (stations 6 to 12) was 0.32 larvae per 10^4 m³; the catch rate in similar CF8503-2 collections (stations 10 to 12) was 0.036 larvae per 10^4 m³.

American eel larvae were somewhat more abundant in positive collections taken south of the southern surface water front during CF8503-2 (stations 10 to 12; 3.2 larvae per 10^4 m³) than they were in similar collections taken during CF8503-1 (stations 7 to 12; 1.0 larvae per 10^4 m³). Similarly, the combined catch rate of recently hatched American eel larvae ≤ 7.5 mm TL at these stations was 0.25 larvae per 10^4 m³ in the CF8503-2 collections and 0.10 larvae per 10^4 m³ in the CF8503-1 collections.

9. Discussion

In these collections the distribution of American and European eel larvae ≤ 7.5 mm TL, which we accept as an indicator of spawning during the preceding three weeks, is limited to the north by the boundary between warm saline surface water of the southern Sargasso Sea and mixed convergence zone water. This result supports the hypothesis that fronts separating northern and southern Sargasso Sea surface water masses form the northern limit of spawning by both Atlantic *Anguilla* species. However, it must be noted that this distribution of small larvae could be the result of one or more mechanisms including the following: (1) *Anguilla* spawn selectively in or

beneath southern Sargasso Sea surface water; (2) *Anguilla* spawn in or beneath both water masses, but their eggs, embryos or larvae are viable only in southern Sargasso Sea surface water; (3) *Anguilla* larvae spawned in or beneath both water masses concentrate themselves in southern Sargasso Sea surface water by a selective behavioral mechanism; and (4) *Anguilla* larvae spawned in or beneath both water masses are concentrated in southern Sargasso Sea surface water by a hydrographic mechanism.

Though we cannot discount totally any of these mechanisms on our data alone, we suggest that the dichotomy in the distribution of small *Anguilla* larvae between the mixed convergence zone and southern Sargasso Sea surface water masses is sufficiently complete to make mechanisms 3 and 4 highly unlikely. Both mechanisms would require the cross-frontal redistribution of larvae spawned within the 100 km to 250 km wide band of mixed convergence zone water into the southern water mass. This movement would have had to occur in the one or two weeks between spawning and the larvae becoming susceptible to sampling.

Active swimming is required for a selective behavioral mechanism to function. *Anguilla* larvae are so morphologically primitive at hatch (Yamauchi *et al.*, 1976) that swimming is limited to rudimentary wriggling (Research Group of Eel Reproduction, 1978). Castonguay and McCleave (1987) have shown that the larvae do not begin a vertical migration until attaining 5 mm TL. Thus, it is highly unlikely that this mechanism would be available to the young larvae prior to their becoming susceptible to sampling.

Passive advection linked perhaps to active depth maintenance could provide a mechanism for selective redistribution of larvae between water masses if the requisite flow were available. Castonguay and McCleave (1987) have shown that *Anguilla* larvae <5.0 mm TL are distributed between 50 m and 300 m. While convergence on fronts separating the mixed and southern water masses could provide persistent southward transport over a few tens of kilometers, and surface currents associated with mesoscale features could transport larvae hundreds of kilometers, there are no reports of persistent southward near-surface flow in the subtropical convergence zone. Rather the region is noted for a high degree of eddy variability resulting in a random pattern of flow (Voorhis *et al.*, 1976). The few larger and therefore older larvae in collections taken north of the southern surface water front in 1985 (Figs. 10B & 11B) suggest to us that even random mixing across the front is limited. The presence of both large and small larvae in the same area south of the front may indicate that there is no systematic pattern of circulation moving larvae away from the front as well.

Both mechanisms 1 and 2 appear equally suitable for explaining the distribution of larvae in these collections based on our data and current knowledge of eel biology. Intuitively we believe that natural selection would favor strongly the evolution of mechanisms permitting identification by migrating adult *Anguilla* of water masses suitable for larval survival. Proof of this ability will likely require a number of indirect tests because of the obvious difficulty in observing directly where adults do and do not

spawn. These tests might include acoustic sampling for concentrations of likely adult targets, identification of these targets as *Anguilla* by remote video or trapping techniques, sampling systematically across a wider range of depths for *Anguilla* eggs, and laboratory tests of adult water preferences and larval survival and growth in different temperature-salinity regimes.

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