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Spawning of American eel, *Anguilla rostrata*, relative to thermal fronts in the Sargasso Sea

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Synopsis

Collections of recently hatched American eel leptocephali including specimens less than 5.5 mm total length suggest the following hypotheses: 1) that thermal fronts separating the northern and southern surface water masses of the Sargasso Sea form the northern limit of American eel spawning, and 2) that some feature of the surface water mass in the southern Sargasso Sea serves as a cue for adult American eels to cease migrating and begin spawning activity.

Introduction

Eels from Europe, *Anguilla anguilla*, and North America, *A. rostrata*, now again documented as distinct species (Comparini & Rodino 1980, Jamieson & Turner 1980, Passakas 1981), spawn during late winter and spring in partially overlapping areas of the southern Sargasso Sea (Schmidt 1925). Although virtually nothing is known concerning the orientation cue(s) utilized by *Anguilla* during their oceanic spawning migration, Ekman (1932) suggested that migrating European eels may identify the spawning area and be contained within its limits by responding positively to the elevated water temperatures found in the upper 300 m in this region of the North Atlantic Ocean. Ekman noted that 'the isotherms for 18–19° C at depths of 200–300 m appear to agree with the boundary assumed by Schmidt for the spawning area' (authors' translation from German).

We have analyzed over 4000 collection records of American eel leptocephali from North American and European oceanographic cruises including those of Schmidt (Kleckner & McCleave in preparation). The smallest leptocephali (26 specimens 7 to 10 mm total length) were collected between the Bahamas and in area of the Sargasso Sea to the northeast, an area in which thermal fronts are found during the late winter and spring (Voorhis & Hersey 1964).

The thermal fronts, which meander in an east-west direction for hundreds of kilometers (Voorhis 1969), are regions of rapid transition between the near surface water mass of the southern Sargasso Sea, with relatively high temperature and salinity, and that of the northern Sargasso Sea, which is seasonally cooled and has lower salinity. The near surface water masses are distinct to depths of 100 to 150 m and are underlain by the North Atlantic Central Water Mass which penetrates to the main thermocline and has uniform temperature-salinity correlations extending over a large area of the Sargasso Sea (Katz 1969, Pickard 1979).

Here we describe the distribution of tiny

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larvae of the American eel in recent collections taken adjacent to a thermal front in the Sargasso Sea, suggest testable hypotheses concerning the relations between *Anguilla* spawning and thermal fronts, and comment on the possible implications of the utilization of this type of oceanic feature by migrating adult eels.

Materials and methods

Between 13 February and 5 March 1981 our group conducted a larval eel survey cruise in the southern Sargasso Sea on the University of Miami's Research Vessel *Columbus Iselin*. Areas of spawning were inferred from the distribution of recently-hatched *A. rostrata* leptocephali. Despite substantial efforts, adults have never been collected beyond the continental slope and eggs cannot be identified with certainty. *A. rostrata* leptocephali were identified by the following: 1) body pigmentation limited to a few melanophores in the caudal fin or absent, and 2) myomeres, including the incomplete pharyngeal series and excluding the extreme caudal segments with fibers not paralleling the main body axis, totaling 102–111. Total length was measured from the anterior tip of the teeth to the tip of the caudal fin rays. Specimens were fixed and preserved in 5% formalin buffered with calcium carbonate. These specimens will be stored in the fish collections of the Department of Zoology, University of Maine at Orono.

Leptocephali were captured in standard oblique tows made with an Isaacs Kidd Midwater Trawl (IKMT) fully lined with 500 μm Nitex netting and having a mouth area of 8.7 m^2. One standard tow was taken at each station. The net was lowered rapidly to its maximum depth and then gradually retrieved to the surface. Standard tow characteristics were (mean ± 1 standard error): maximum depth $= 298 \pm 9$ m, time to maximum depth $= 23 \pm 1$ min, retrieval time $= 92 \pm 2$ min, ships speed ~ 3.5 km h^{-1}. The average volume of water filtered, estimated from five tows in which digital flow meters functioned properly, was 4.89×10^4 m^3 (range $= 4.42$ to 5.20×10^4 m^3).

Satellite imagery was used to locate the region of the thermal front shown in Figure 1. Starting on the cold, northern side of the front at trawl station 17 we collected samples along a transect which crossed to the warm side and then paralleled a cold plume of the front. Station 21 was taken in a tongue of cold water near the southern end of the cold plume. The remaining stations were all taken on the warm side of the front.

Results

The range of horizontal temperature change across the front was greatest in the near surface layer. Surface temperature changed by up to 2.5° C during passage across the front between stations 17 and 18, 20 and 21, and 21 and 22 (Fig. 2). Corresponding temperature changes at 150 m and 200 m were reduced to amplitudes of 1.5° C and 0.8° C respectively. Fluctuations of less than 0.5° C occurred below 300 m.

American eel leptocephali including specimens 3.9 mm to 5.5 mm total length were collected at stations 18 to 20, 22, and 26 to 28 on the warm side

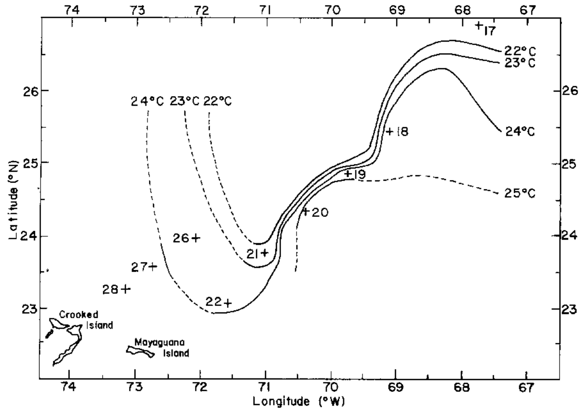

Fig. 1. Horizontal plot of surface isotherms and IKMT stations (+) made between 25 and 27 February 1981. Solid isotherms are based on measurements made with a continuous recording thermograph, the water source for which was located on the forward part of the ship's hull at a depth of 2 m. Dashed isotherms are extrapolations based on satellite imagery. Stations 23–25 were not IKMT stations. Stations 26–28 were offset to avoid Mayaguana Island, southwest of our initial transect.

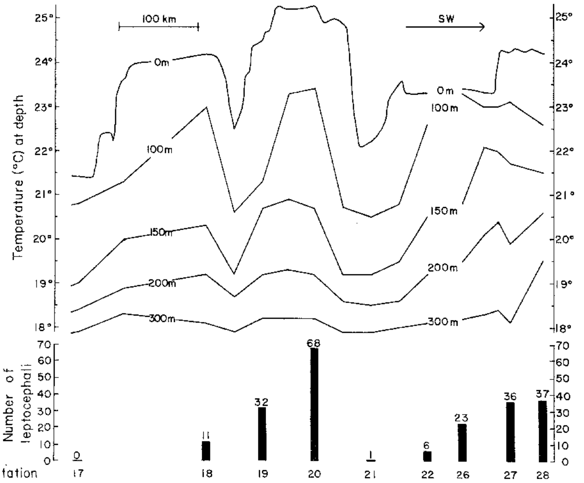

Fig. 2. Plots of temperatures at selected depths and number of *Anguilla rostrata* leptocephali in standard IKMT tows along the thermal front. Rapid vertical excursions in the temperature profiles indicate regions where the thermal front was crossed. Surface temperature is based on continuous thermograph recordings described in Figure 1. Subsurface temperatures are based on expendable bathythermograph profiles.

of the front (Fig. 2). The mean length of these specimens was 8.3 mm (standard error = 0.15 mm). No American eel leptocephali were collected at station 17 on the cold side of the front. One American eel leptocephalus, measuring 6.0 mm total length, was collected at station 21 on the cold side of the front. The eyes of this shriveled specimen are brown; those of American eel leptocephali in the other collections are black.

Discussion

American eel leptocephali were abundant at most of the stations located on the warm side of the front while they were rare or absent on the cold side. The one specimen taken at station 21 may have been spawned north of the front or it may have remained trapped in the net following the preceding station. The latter explanation seems probable because its eyes would have been bleached by sunlight as the net lay on deck between stations.

All positive collections on the warm side of the front included American eel leptocephali of less than 5.5 mm total length. Though nothing is known about the growth rate of recently hatched *A. rostrata*, artificially spawned *A. japonica* hatch in less than 48 h and attain a length of about 6 mm five days after hatching (Yamamoto & Yamauchi 1974). Considering the close affinities of the two species (Ege 1939), it is reasonable to assume a similar growth rate for both. Therefore it is probable that spawning occurred within one week of our sampling at these locations.

The leptocephali in our collections all showed incomplete development of the caudal myomeres which form part of the main propulsive mechanism. It is unlikely that they would be capable of selectively altering their horizontal position relative to the front. The sharp density gradient measured between adjacent water masses at a front is maintained in part by currents running parallel to the frontal surface (Voorhis & Hersey 1964, Katz 1969). Therefore, it is unlikely that leptocephali would have been transported passively across the front.

Clearly, American eels had spawned on the warm side of the front shortly before we took our collections. Unfortunately, our collection effort on the cold side was too low to allow us to state with certainty that spawning did not take place on the cold side of the front. We believe that the distribution of American eel leptocephali in these collections does support the following testable hypotheses: 1) that thermal fronts separating the northern and southern surface water masses of the Sargasso Sea form the northern limit of American eel spawning and 2) that some feature of the surface water mass in the southern Sargasso Sea serves as a cue for adult American eels to cease migrating and begin spawning activity.

The correlation between the apparent limit of spawning and the presence of the 18–19°C isotherms between 200–300 m noted by Ekman (1932) for the European eel spawning area appears to hold for the American eel as well. Though a correlation exists, we believe it to be unlikely that migrating adults could sense the gradual change in temperature occurring in the North Atlantic Central Water Mass at 200 to 300 m (Fig. 2) with sufficient acuity to produce such a distinct pattern of positive and negative trawl stations obtained in our transect along the thermal front. Rather, the cue is likely in the surface waters, because the complex pattern formed by the thermal front does not extend to deeper levels (Katz 1969). We believe that a thermal, chemical or other characteristic of the surface water mass south of the front acts as a cue triggering the cessation of migration and the initiation of spawning behavior. Combined with a depth preference governed by a light, hydrostatic or other cue, the front may act to concentrate migrating adults within an otherwise enormous oceanic volume, for spawning.

Similar cues could also be used by migrating European eels, as the spawning area determined by Schmidt (1925) for this species lies within the area of thermal front activity (Voorhis & Hersey 1964). European eel spawning, which peaks in April, is centered to the northeast of American eel spawning, which peaks in February (Schmidt 1925). The latitudinal variation in spawning locality between species may be related to an apparent northward shift in the position of the thermal front (Schroeder 1965) as the surface layer warms and becomes stratified during the spring. Further field work is needed to test this hypothesis and to provide further insight into how currents in the spawning areas effect the initial phases of larval transport toward North America and Europe.

Backus et al. (1969) argued that a thermal front in the Sargasso Sea acts as a boundary for a variety of species including teleost fishes, phytoplankton, Foraminifera and Radiolaria. They suggested that these differences in species composition are caused by a marked decrease in primary productivity south of the front. This decrease is attributed to the absence of seasonal mixing in the permanently stratified surface water mass of the southern Sargasso Sea (Ryther & Menzel 1960). Colton et al. (1975) observed that the front persists through the summer at depths between 50 and 150m even though its surface manifestations are obscured. The reduction in primary productivity, combined with the seasonal stability of this layer, may provide a variety of persistent olfactory cues, distinct from those of the northern water mass, for eels returning to spawn after many years in fresh water.

The depth at which adult *Anguilla* migrate to the spawning area is open to question. The only direct evidence is the sighting of one or possibly two eels on the bottom at a depth of 2000 m within the Bahama Island chain (Robins et al. 1979). Interestingly, all indirect evidence suggests that migratory adults are adapted morphologically and physiologically for swimming and spawning at significantly shallower depths. Dramatic increases in eye diameter (Winn et al. 1975) and changes in visual pigment composition (Beatty 1975) just prior to offshore migration, which adapt eels for vision in dim blue light, would be adaptive only in the photic zone. An increase in capillary length in the rete mirabile of the swimbladder during the premigration change (Kleckner & Krueger 1981), gives *A. rostrata* retial capillaries comparable in length to those of Macrouridae common at depths between 150 and 800 m (Marshall 1972). Retial capillary length is related to the depth of occurrence in epi-, meso- and bentho-pelagic teleosts (Marshall 1960, 1972, Wittenberg et al. 1980). Experimental evidence on the maximal depth for the maintenance of swimbladder volume (Kleckner 1980) and the optimal temperature for final gonad maturation (Boëtius & Boëtius 1967), indicate that eels are adapted for migration and spawning in the upper 200 m of the water column. Our data may be added to this list, as supporting a relatively shallow migratory route for *Anguilla* during the last phase of the spawning migration.

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