OCEANIC ENVIRONMENTS OF THE GENUS *ENGRAULIS* AROUND THE WORLD

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THE GENERAL AREA INHABITED BY *ENGRAULIS*

The areas where the genus *Engraulis* is known to occur are shown approximately in Figure 1. It is seen to be limited to coastal areas in general. Dr. Ahlstrom has reported spawning of *Engraulis* as far as 200 miles offshore in the California Current. This is in a particular region off southern California where the currents are such that the eggs and larvae will subsequently be brought much closer to the coast, along northern Baja California. Although eggs have been found as far as 1000 miles offshore from Japan it seems likely that these have been swept away from Japan by the Kuroshio and have little chance of surviving long enough to return to the ordinary Japanese habitat.

The genus has been found to extend to latitudes as high as 60°N and 43°S at least in summer. It is found in all of the eastern boundary currents (California, Peru, Canary, and Benguela currents, and off western Australia) in three of the western boundary currents (Kuroshio, East Australia, and Brazil), though not in the Gulf Stream or Agulhas Current. It occurs also in the Sea of Japan, the area south of Australia, around the northern part of New Zealand, and in the Mediterranean and Black Sea. In summer it extends into the North Sea, the Baltic, and the Sea of Azov, but retreats from these areas when they become extremely cold in winter, though it does remain in the Black Sea throughout the year.

CHARACTERISTICS OF THE DIFFERENT AREAS

The eastern boundary current areas are cooler and lower in salinity than the central ocean waters at the same latitude. They are usually characterized by up-

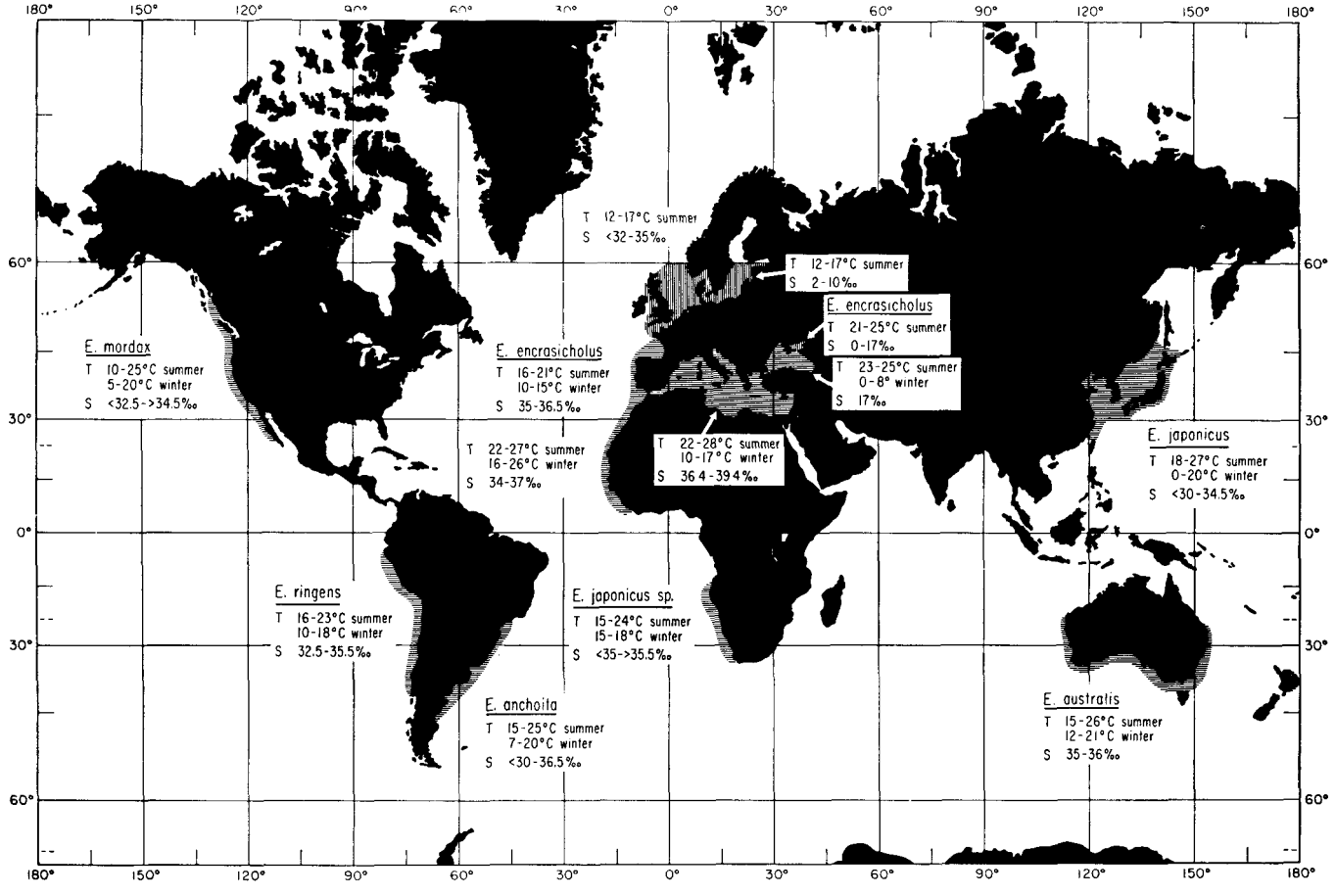

FIGURE 1. Areas inhabited by *Engraulis*.

welling in temperate latitudes and are richer in nutrients and higher in productivity and zooplankton volume than the central ocean waters. In temperate latitudes the depth of the mixed layer is notably shallower in the eastern boundary currents than further offshore.

The western boundary current areas in temperate latitudes are warmer than the central water masses. They are not so rich as the eastern boundary currents but are richer than the central ocean. Zooplankton volume is moderate. The mixed layer is much thicker than in the eastern boundary currents.

The North Sea is a tolerable environment in spite of its high latitude only because it receives some water from the south via the North Atlantic Current and the Gulf Stream: it is therefore much warmer than any other water at this latitude. It is shallow, much of it less than 100 m in depth, and fairly well mixed, so that it does not offer a wide range of properties, though the vertical mixing and advection render it fairly productive.

The Baltic is still shallower and much fresher, the salinity of the surface water decreasing almost to zero in the upper reaches and even the few deeper basins contain water of only about 12‰ at the bottom.

THE RANGE OF TEMPERATURE AND SALINITY IN THE HABITAT OF *ENGRAULIS*

The Mediterranean is a much more nearly homogeneous body of water than is the adjacent part of the Atlantic. Salinity is everywhere quite close to 38.5‰ and the temperature, except for the thin summer-warmed layer, is near to 13°C. Because of the extreme evaporation over the area the water is very saline and dense, and overturn to the bottom occurs in part of the Mediterranean. Exchange with the Atlantic occurs by outflow of saline water to the deeper part of the Atlantic, and inflow of surface water from the Atlantic. For this reason the nutrient concentration in the Mediterranean is low and productivity is generally low.

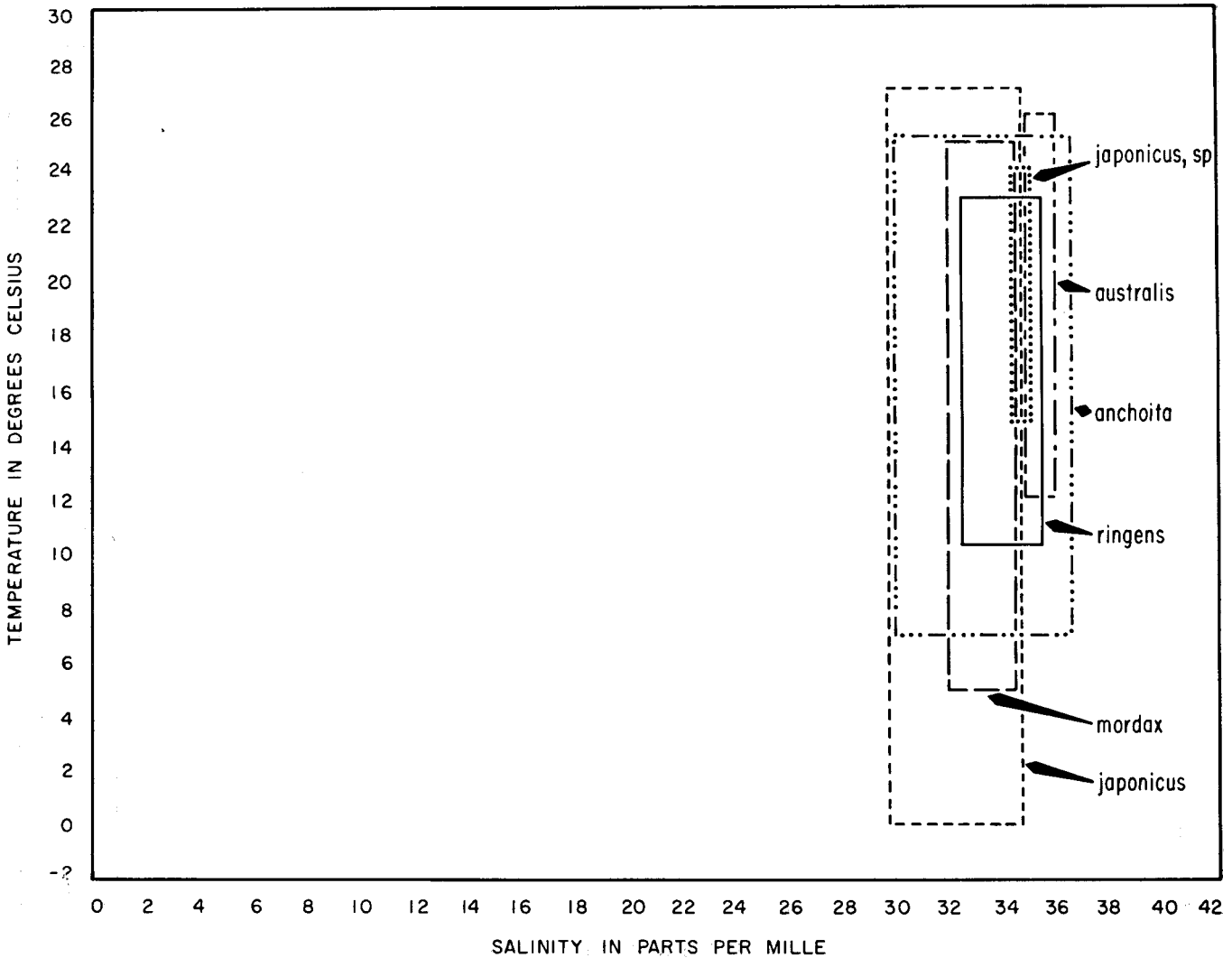

FIGURE 2. Temperature and salinity ranges of areas inhabited by *Engraulis*.

The Black Sea is the most curious habitat of *Engraulis*. Surface waters are maintained at such a low salinity that overturn to the bottom does not occur in the Black Sea, and exchange of the deeper waters with the Mediterranean is limited by the intervening sill. As a result the deeper water of the Black Sea is but slowly renewed and is devoid of oxygen below about 200 m depth: large concentrations of hydrogen sulphide are found beneath this level. *Engraulis* is therefore confined to a shallow level that is not enriched by overturn to great depth.

The Sea of Japan is fed by a flow from the south of relatively warm and saline water: this flows up the eastern boundary of the Sea, is cooled and diluted, and returns as much colder and less saline water. This and the effect of season give the Japan Sea a wide range of properties, from the freezing point in the northwestern region in winter to the warm values of the Kuroshio in the southeast in summer.

The areas inhabited by *Engraulis* include not only the oceanic areas roughly indicated in Figure 1, but include also the very shallow inshore waters and bays, lagoons, and estuaries. The values of temperature and salinity that are shown on Figure 1 represent only the oceanic part of *Engraulis'* habitat: somewhat higher and very much lower values of salinity and temperature would appear if the inshore, non-oceanic habitats were included. Note also that for the Baltic, North, and Azov seas only the summer values are shown: apparently *Engraulis* retreats from these areas when they become very cold in winter. Surface temperatures in the Baltic are between 0 and 2°C in winter, in the North Sea between 2 and 7°C, and in the Azov Sea between 2 and 3°C. It is also noteworthy that *Engraulis* remains in the Black Sea throughout the winter when surface temperature is about 8°C.

Those figures do not take into account in any complete way the migrations, either horizontal or vertical, that *Engraulis* may make in response to seasonal changes in the environment. Therefore the values undoubtedly include a somewhat wider range

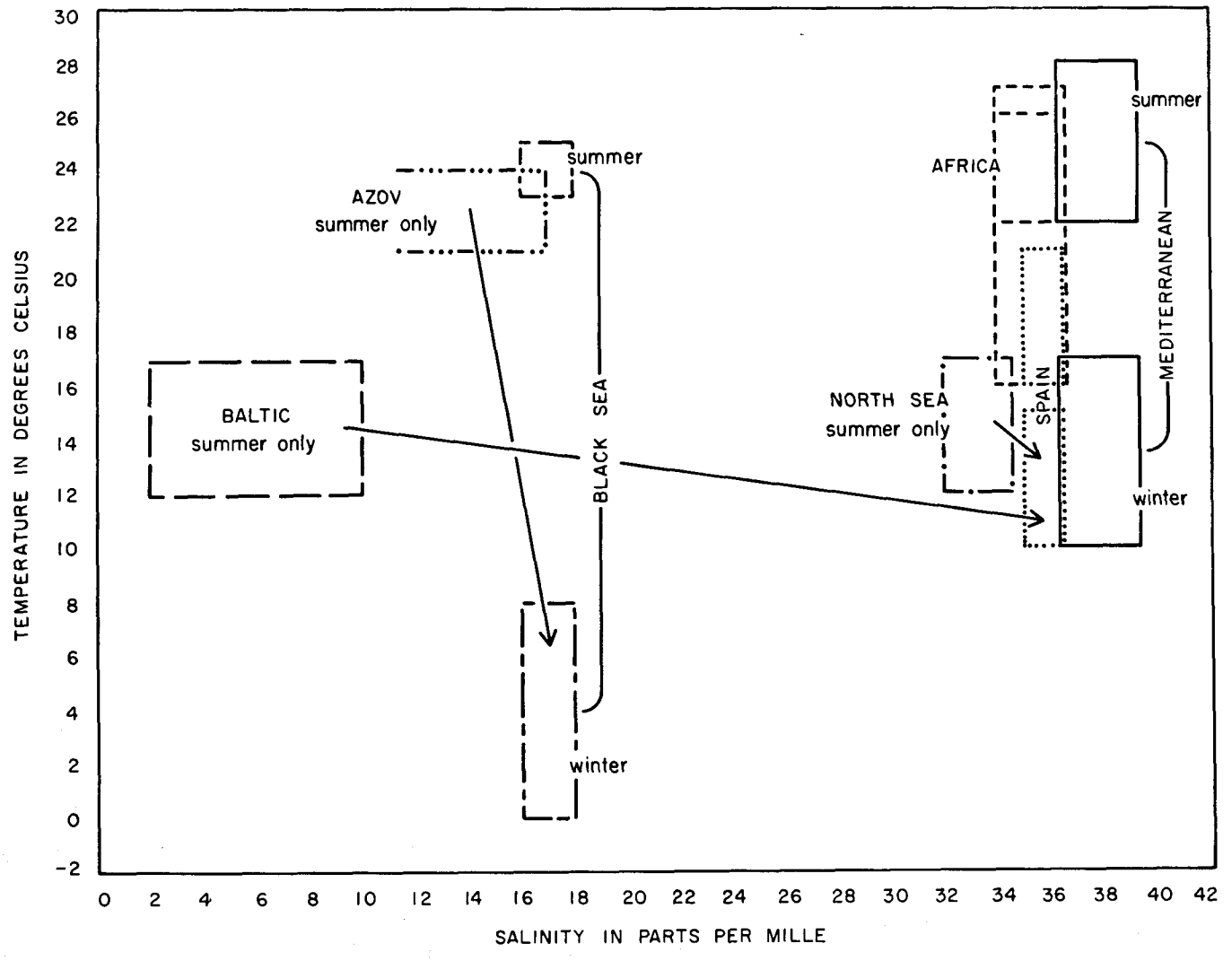

FIGURE 3. Temperature and salinity ranges of areas inhabited by *Engraulis encrasicholus*.

of temperature than the animal actually experiences. One conspicuous example of how misleading such a simple diagram might be is found in the Mediterranean. Summer surface temperatures are from 22° to 28°C and winter values are from about 10°C to 17°C. There is no overlap. On the other hand, we know that these very high surface temperatures in summer are restricted to the upper few meters, and that by being as little as 15 m beneath the surface the fish might easily find temperatures less than 22°C everywhere, even in August. This may apply in many of the other areas as well in summer, so that the upper limit of surface water temperature may not represent the temperature the fishes experience. Likewise, Dr. Hayasi reports, the fish avoid the extremely low water temperatures of the northern Sea of Japan in winter by staying in the southern area, which is much warmer. On the other hand, in some areas the winter temperatures are inescapable. Fishes in the Black Sea in winter must undergo temperatures of about 8°C: there is no warmer water anywhere in the Black Sea at that time.

On Figures 2 and 3 these open-ocean ranges of surface temperature in winter and summer are shown as rectangles with temperature as the vertical scale and salinity as the horizontal scale. In both cases the entire range of oceanic values of temperature and salinity is shown in order to emphasize the proportion of these ranges that *Engraulis* occupies. All except one of the species are included on Figure 2: *E. encrasicholus'* range is much wider and is shown separately on Figure 3.

Figure 2 would seem to indicate that the oceanic habitat of *Engraulis* comprises almost the entire range of temperature in the ocean but only a small part of the salinity range. This would be a very wrong inference indeed. Baxter (p. 110) and others have shown that *Engraulis* retreats to offshore and deeper water to avoid some extremes of temperatures; the total range, which includes extreme summer surface temperatures that the fishes may avoid by a slight submergence, and the extreme winter temperatures in the northern part of the Sea of Japan that the fish may avoid by moving a short distance to the south, may be quite misleading. On the other hand, it has also been shown that the fish do move into the quite brackish waters of bays and estuaries when the temperature is not too extreme. Therefore, all of these rectangles should extend an uncertain distance to the left on the graph to include, at least during some part of the year, waters of very low salinity indeed. This is emphasized in Figure 3 by the ranges of *E. encrasicholus*. The open-ocean values from the North Sea southward past Spain to western North Africa look very much like the ranges on Figure 2 of the other *Engraulis* species. But the ranges in the Baltic, the Mediterranean, the Black Sea and the Sea of Azov emphasize the real capability of *encrasicholus* to endure almost-fresh as well as extremely saline water and very cold water. It is apparently the seasonal change in temperature that causes them to leave the Baltic, North and Azov seas, since the salinity does not change very much with season.

Looking again at Figure 2, some of the open-ocean salinity ranges appear to be very narrow. This signifies that the total range of offshore salinity values in the *Engraulis* habitat is small, not that *Engraulis* is limited to a narrow range of salinity, since we know that it occurs in brackish waters. It appears that *Engraulis* can endure the total range of salinity encountered in the open sea, including the Mediterranean values above 39‰, but may be limited to only part of the temperature range. Various investigators who are better informed may correct me, but it seems possible that *Engraulis* may actually not experience temperatures much below 7 or 8°C, though it may experience these in many areas besides the Black Sea. Resident populations of *E. mordax* near Vancouver Island will experience 7 or 8° in winter and if *E. anchoita* and *E. enchrasicholus* do not retreat completely from the Falkland Current and North Sea areas some of the individuals will undergo values of about 8°C or less.

In winter *E. encrasicholus* is found only at temperatures less than 18° and it may by a slight submergence in summer avoid temperatures more than 22°C.

Blackburn (this symposium) has shown that *E. australis* occurs only between about 10°C and 20°C, and Ahlstrom (1956) has said that most of the eggs and larvae of *E. mordax* have been taken in about that range, though some have been taken at more than 23°C. The total range of the area occupied by *E. ringens* is from about 10°C to 23°C, and this includes north to south and winter and summer: slight migrations might reduce this appreciably.

E. japonicus capensis simply has no opportunity to endure cold water: about 15°C is the lowest surface temperature he may encounter at the tip of Africa, which is only about lat. 35°S. Likewise, a population of *E. encrasicholus* that remains in the Mediterranean may not find water colder than 10°C at any time of year.

CONDITIONS LIMITING *ENGRAULIS*

We may speculate, then, that *Engraulis* is not limited by the salinity values encountered in the ocean or in estuaries: it not only occurs but spawns in regions of very low as well as very high salinity. We may speculate also, at least until the other speakers correct me, that *Engraulis* is limited by temperature, since it does not appear in either the coldest or the warmest oceanic conditions. Perhaps a range from 6°C to 22 or 23°C would include all, or nearly all, of its actual occurrences. This would account for its limited latitudinal range and for its most striking migrations from the Baltic, North, and Azov seas, whereas salinity variations would not.

This really does not add very much to what most of you know already, and it does not by any means specify the habitat of *Engraulis*. By this I mean to say that there is a vast area of ocean with surface temperature between 6°C and 22°C—about $\frac{3}{8}$ of the world ocean, in fact—but that *Engraulis* inhabits, so far as we know, less than $\frac{1}{10}$ of this area. Therefore temperature alone cannot define the habitat of *Engraulis*.

What are some of the other quantities that might be important to *Engraulis*, and that might explain their absence from other areas that seem to have the proper temperature and salinity?

First, it appears to be a coastal genus. Such information as I have got so far indicates that although eggs and larvae are sometimes found some hundreds of miles offshore they are definitely tied to a coastal population—that is, they do not appear in areas separated from the coast. I do not know how to interpret this. I have consulted several biologists and have concluded that there is no single, generally accepted explanation as to what there is about coasts that appeals to some nekton.

It is true that most coastal regions are somewhat more productive than the offshore temperate-zone areas, but the genus can inhabit the Mediterranean, where productivity is fairly low. The region near the equator and at some distance west of South America fits the temperature requirements of *Engraulis* and is extremely productive, yet *Engraulis* does not appear to be found any great distance offshore there. Likewise there are other offshore temperate-zone areas of relatively high productivity such as the region around lat. 45°N in the Pacific that *Engraulis* does not inhabit. Therefore temperature and productivity are not enough for *Engraulis:* there has to be a coast nearby—perhaps some place where the bays, lagoons or estuaries or the inshore countercurrents and turbulence may provide a firm foothold for a population, so that it is not swept entirely away by the prevailing currents, as it might be in the truly pelagic areas.

Having accepted coasts and a particular temperature range as requirements for *Engraulis,* whether we can explain the relation or not, we have eliminated most of the ocean as habitable areas for *Engraulis.* We find that what is left, that is, coastal waters with temperature ranges between about 6° and 22°C, is in fact inhabited by *Engraulis* except for one conspicuous omission: the eastern coast of North America. In August the temperature range from 6° to 22°C is found between Labrador and New York, in February between New York and Cape Hatteras. The area of overlap is small but so is it in some of the other habitats: a minor amount of seasonal migration could keep *Engraulis* at optimum temperatures throughout the year in this general region. If inshore habitats are required this coast has plenty of estuaries and sounds that would seem to compare favorably with those of the other coastal areas inhabited by *Engraulis;* I cannot offer any speculation as to why *Engraulis* does not inhabit this area.

REFERENCES

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