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The Distribution of Mesopelagic Fishes in the Equatorial and Western North Atlantic Ocean[1]

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ABSTRACT

Examination of about 290 midwater trawl hauls made to a depth of 1000 m in the equatorial and western North Atlantic Ocean from 1961 to 1968 suggests that at least 10 physical boundaries determine the ranges of mesopelagic fishes. The boundaries delimit six pelagic regions—the Slope Water Region, the Northern Sargasso Sea, the Southern Sargasso Sea, the Gulf of Mexico, the Caribbean Sea, and the Amazonian Region— and partly delimit four others—the Eastern Gyre and the Labrador, Lesser Antillean, and Guinean regions. It is rare for a fish species to be restricted to a single region. Rather, the fish distribution patterns noted result mainly from the occupancy of various combinations of regions by species. For warm-water species, seven distribution patterns have been noted, the most important of which are the *tropical*, the *broadly tropical* and the *Sargasso Sea* patterns. We have insufficient data for defining the distribution patterns of widespread species and species having essentially eastern and northern ranges in the North Atlantic. Each of these categories contains species that are distributed according to more than one pattern, and species in the northern group are tentatively divided into three subgroups on the basis of the southern range limit in the west. Each pelagic region has a more or less unique fish fauna with its characteristic assemblage of species in characteristic proportion, its characteristic diversity, and so on. Zoogeographically, the equatorial and western North Atlantic consists of a northern part (north of 35° N or 40° N) and a tropical part (the Gulf of Mexico through the Guinean Region), separated by a broad transition zone (the Sargasso Sea).

Introduction. Sampling the fishes of the mesopelagial, the dimly lit upper midwaters of the open ocean between about 100 and 1000 m, is difficult. Like all fishing gear, midwater nets are selective. Moreover, most mesopelagic species are daily vertical migrators, and there is evidence (e.g., Clarke and Backus 1964) that they are continually altering their depth, although most of

the change comes at dusk and at dawn. Furthermore, the physical factors that appear to control the depths at which these fishes lie (transparency, temperature, and the like) vary horizontally over distances of a few miles. In short, the arrangement of fishes in the water column is continually changing from moment to moment and from place to place.

It is for this reason, as well as for the sheer size of the area involved, that so little is known about the patterns of geographic distribution of North Atlantic mesopelagic fishes (or of any group of mesopelagic organisms in any ocean). Even less is known, of course, about what the physical factors controlling these distributions might be, although what can be called the "water mass" hypothesis is currently popular. This useful idea suggests that the ranges of pelagic animals conform to the water masses as defined by their temperature-salinity relationships. This concept was first used by Pickford (1946) and Haffner (1952) and has grown mostly as a result of Pacific Ocean studies (e.g., Bieri 1959, McGowan 1960, Brinton 1962, Ebeling 1962, Fager and McGowan 1963, Ebeling and Weed 1963, and Paxton 1967). Were the water mass hypothesis sufficient, however, the zoogeography of the North Atlantic pelagial would be very simple, for it consists almost wholly of one water mass—the North Atlantic Central Water. Our data indicate a far greater complexity, and we offer here some generalizations about the distribution of mesopelagic fishes in the equatorial and western parts of this ocean.

Collecting Methods and General Description of Collections. The principal data come from about 290 midwater collections made from the Research Vessels CHAIN and ATLANTIS II between 1961 and 1968 along the transects shown in Fig. 6. Most of the collections were made with the 10-foot (3.05 m) Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd 1953). The mouth of the standard 10-foot IKMT is about 7.9 m²; the bag is made of 63.5-mm (stretch) netting, with a 12.7-mm (stretch) liner in the rear. Recently we have used nets that are fully lined, with 12.7-mm mesh in the forward part and 9.5-mm mesh in the rear part. No adequate comparison has been made of the relative "catching power" of the two nets, but a small amount of data suggests that the fully lined net catches two to three times as many specimens per unit of effort as the half-lined net. In all cases a one-meter plankton net with 0.75-mm openings has been fitted to the cod-end of the trawl. The towing time per haul has ranged from two to four hours at a speed of about three knots. Net depth in most cases was measured by a time-depth recorder (Benthos Co.) attached to the trawl, but sometimes it was determined by triangulation (measuring wire angle and amount of wire out); the latter procedure is justifiable with towing warps of moderate length because the effect of the IKMT depressor is to take the belly out of the wire (Backus and Hersey 1956). Recently, net depth has been controlled by means of a telemetering depth meter (Benthos Co.).
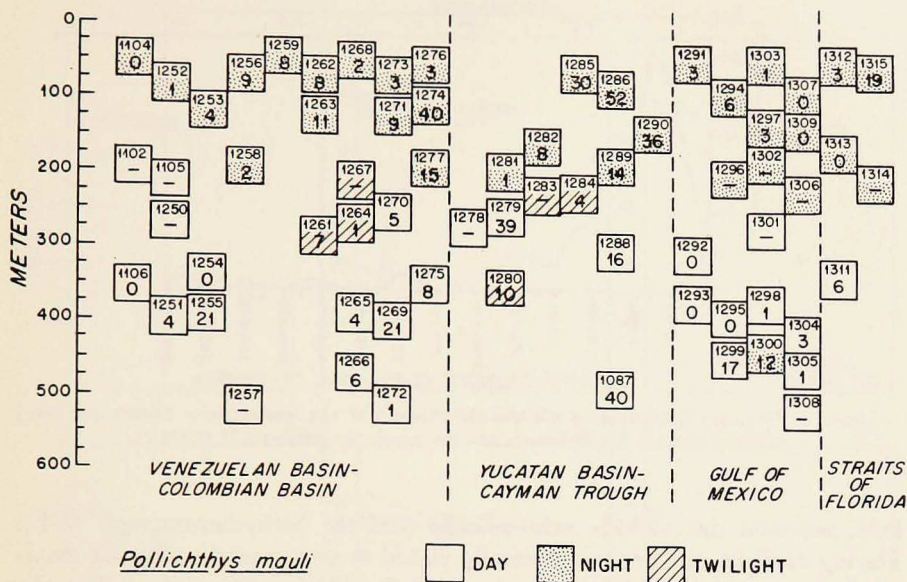
Figure 1. Sample of a worksheet showing the distribution according to depth and time of day of mid-water trawl collections made on CHAIN Cruise 60 and upon which have been plotted captures of the gonostomatid *Pollichthys mauli*. The upper numbers within the boxes are collection numbers, the lower ones, numbers of specimens.

Most of the samples have been collected in the upper 600 m, a few between 600 m and 1000 m. Daytime tows generally have been made at depths greater than 200 m. Shallower daytime hauls catch little or nothing, partly because most mesopelagic species lie at greater depths by day and partly because fish avoid the net when it is well illuminated (Pearcy and Laurs 1966). Night-time tows generally have been made at depths shallower than 300 m because many of the abundant mesopelagic species migrate at sunset to depths above this level. Hauls at twilight, when animals are vertically migrating rapidly, generally have been avoided; when made, the net has been towed between 200 m and 300 m, near the top of the range of our daytime tows and near the bottom of the range of our night-time ones. Because no opening-closing device has been used on the net, a haul may have been contaminated to some extent with specimens caught while the net was being set and hauled back. The time consumed in setting and retrieving the net has generally been less than 20% of the total time of the tow. The depth distribution of tows made on a representative cruise is shown in Fig. 1.

In planning the sampling, approximate depths of tow were chosen so that a few successive tows would more or less cover the upper 600 m of the water column before the ship had changed geographic location too much. More refined sampling depths were chosen so as to catch as much as possible. For
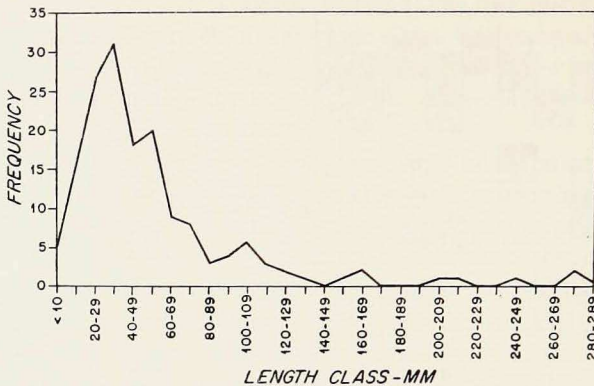
Figure 2. Frequency distribution of the maximum lengths of 155 species (about 80,000 specimens) collected between Massachusetts and the Azores on ATLANTIS II cruise 13.

help, we used the 12 kHz echo-sounder and the bathythermograph (BT). During daylight, the net was generally placed at some sound-scattering maximum (in a so-called "deep scattering layer"). During the night, when the animals sought are in that part of the water column where marked changes in temperature occur with depth, both the echo-sounder and the BT have been used. Experience has shown that sound-scattering maxima, temperature inversions, and the bottom of thermoclines and surface isothermal layers mark planes of concentration of midwater fish.

A few species of mesopelagic fishes migrate at night to the very sea surface. We have mainly caught these species in neuston nets (Bartlett and Haedrich 1968), which sample the upper 10 cm or so. Generalizations about the distribution of nine species (*Astronesthes niger, Centrobranchus nigroocellatus, Gonichthys coccoi, Myctophum affine, M. asperum, M. nitidulum, M. obtusirostris, M. punctatum,* and *Symbolophorus veranyi*) are based principally upon material taken in about 115 neuston net hauls.

The fish in each collection have been sorted according to species and identified. For each species lot, the number of specimens, range of standard lengths, and displacement volume have been determined.

There is no good estimate of the distribution of sizes of the fish in the mesopelagial. It is certain, however, that many are large enough to easily elude our nets. On the other hand, it is equally well established that many mesopelagic species become sexually mature at a size as small as 25–50 mm in standard length (see, for instance, Tåning 1918, Grey 1964, and Nafpaktitis 1969). Thus, in spite of the fact that most of the fish that we have captured are small (Fig. 2), adults and subadults of many species are included, especially from among the abundant and speciose families Myctophidae and Gonostomatidae.
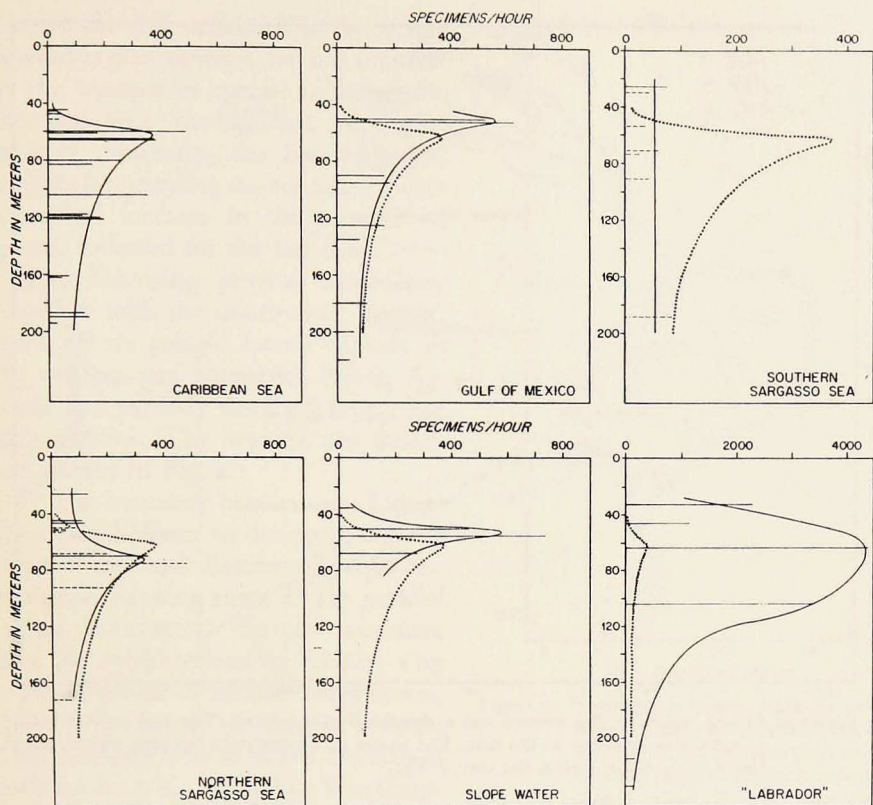
Figure 3. Number of specimens collected per hour in night-time collections in six pelagic regions of the North Atlantic plotted as a function of depth. The curves have been fitted by eye. The broken lines indicate catches that came from half-lined nets; these catches were doubled before plotting. The curve for the Caribbean Sea is used as a standard and is repeated as a broken line in the plots for the Gulf of Mexico, Southern Sargasso Sea, Northern Sargasso Sea, and the Slope Water and Labrador regions.

Both the number of specimens caught and the displacement volume per unit of effort have varied widely. Fig. 3 shows some of this variation in night-time collections and its relation to depth of tow and ocean region. The analysis of the relative abundance of species to one another as a function of region is made difficult by the region-dependent variation in the total amount of material caught.

The number of species taken in a collection has varied from fewer than 10 to several dozen. If the composition of a group of collections from a single ocean region is considered, it is seen that only a few species are abundant while many are rare.

After excluding from our collections epipelagic species and the young of certain littoral and benthic species that are only temporary inhabitants of the
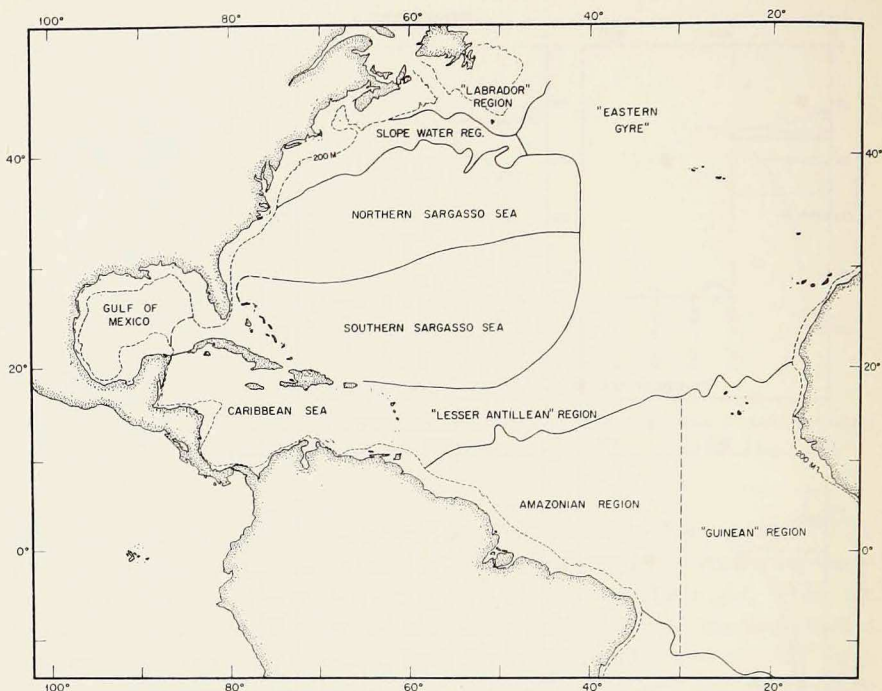
Figure 4. Pelagic regions of the western and equatorial North Atlantic. The broken lines indicate uncertainties described in the text. The names of incompletely bounded regions are enclosed in quotation marks. See text, p. 185.

pelagial, about 350 species remain to be considered. Only about 80 of these have occurred in our collections with enough consistency so that we can remark upon their distribution with some confidence. Of these 80, three-fourths belong to the families Myctophidae and Gonostomatidae.

Faunal Boundaries and Pelagic Regions. Our collections show that the 10 physical boundaries listed below have significance as faunal boundaries for mesopelagic fishes. In some cases, we assumed that a physical boundary had significance as a faunal boundary and then designed a cruise to test the hypothesis (especially numbers iii and v below). In other cases, faunal changes within transects were noted only after collection and study of the data. In these, if a faunal change was correlated with a physical change, the physical boundary was taken as the faunal boundary.

In order to objectively examine collection transects for faunal changes, we have developed a method of analysis based upon the distribution of the first and last captures of species within the transect (Backus et al. 1965). This method is based upon the simple principle that when a faunal boundary is

crossed the first collection in the newly entered region shows a marked increase in the number of species collected for the first time during that particular transect. Similarly, the last collection made before crossing the boundary shows a marked increase in the number of species collected for the last time.

The following physical boundaries (together with the continental margin) mark off six pelagic faunal regions in the western and equatorial North Atlantic and partially mark off four other such regions. The regions are shown and named in Fig. 4.[2]

i. The boundary between the Labrador-Coastal Water to the north and the Slope Water and Eastern Gyre to the south and running more or less parallel to the continental margin westward from the neighborhood of Flemish Cap to the longitude of central Nova Scotia, where it intersects the 200-m isobath. This boundary is set to follow the 200-m isotherm for 9°C. We follow Worthington (1964) in choosing this isotherm and Schroeder (1963) in drawing it.
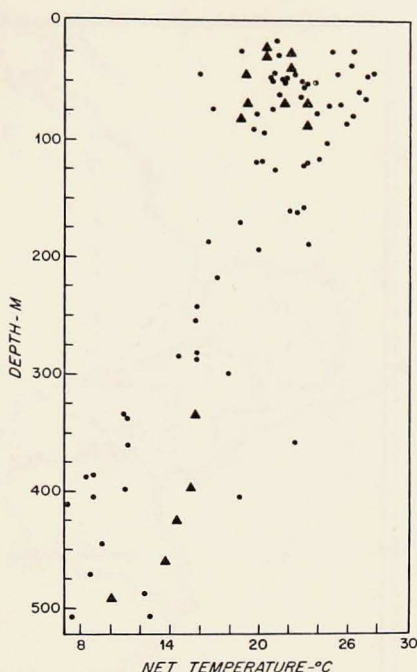

Figure 5. Temperature versus depth for collections including *Pollichthys mauli* (solid dots) and for collections over a similar range of depths in pelagic regions where *P. mauli* does not occur (triangles).

ii. The boundary between the Slope Water to the north and the Gulf Stream and northern Sargasso Sea to the south. This boundary follows the 200-m isotherm for 15°C. Worthington (1964) is followed in choosing this isotherm, and Schroeder (1963) is followed in drawing it.

iii. The boundary between the two North Atlantic clockwise gyres first described by Worthington (1962)—the southwestern (Sargasso Sea) gyre with Bermuda near its center and the northeastern gyre. The boundary follows the trough between the two gyres, running southeastward from the tail of the Grand Bank and connecting i and ii.

iv. The perimeter of the Sargasso Sea as defined by the temperature-salinity characteristics given by Worthington (1959). This boundary is used with ii to circumscribe completely the Sargasso Sea and begins at the junction of ii and iii, runs east to about 40°W, then south, southwest, and west to end near Puerto Rico.

2. The various attempts at dividing the world ocean into regions have been summarized by Laevastu (1963). None of the North Atlantic schemes bears much resemblance to ours.
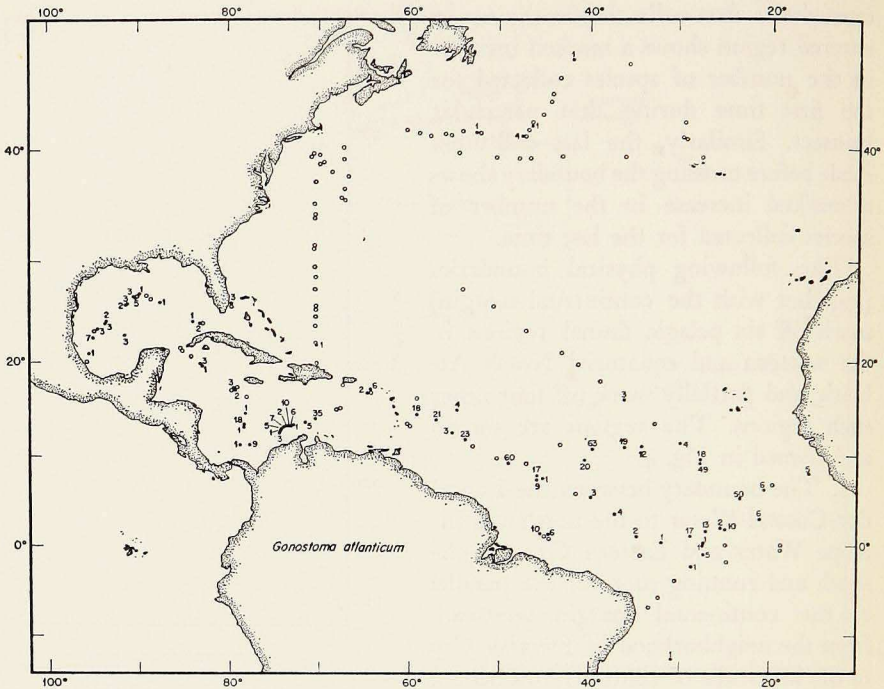
Figure 6. Distribution of *Gonostoma atlanticum* showing the *tropical* pattern. The numbers next to the solid dots show the number of specimens taken; these numbers have not been adjusted for variations in collection duration or for variations in net construction. A circle indicates that no specimens were taken in a collection at a depth deemed appropriate.

v. The boundary corresponding to the area of the so-called thermal fronts (Voorhis and Hersey 1964), which may be the same as the North Atlantic Subtropical Convergence (Katz 1969); the boundary in Fig. 4 has been drawn as the convergence is commonly drawn following Neumann and Pierson (1966: 425). This boundary divides the Sargasso Sea into northern and southern parts, the northern part being in the upper few hundred meters cooler, less stable, and more productive than the southern part (Backus et al. 1969).

vi. The boundary corresponding to the usual topographic limits of the Gulf of Mexico, except around the western end of Cuba, where the boundary is drawn to exclude from the Gulf of Mexico the region of strongest current. Because this last part of the boundary is not rigorously defined it is drawn with a broken line.

vii. The boundary corresponding to the usual topographic limits of the Caribbean Sea.

viii. The boundary between the North Atlantic Central Water and South Atlantic Central Water. This boundary is set to follow the 200-m isotherm
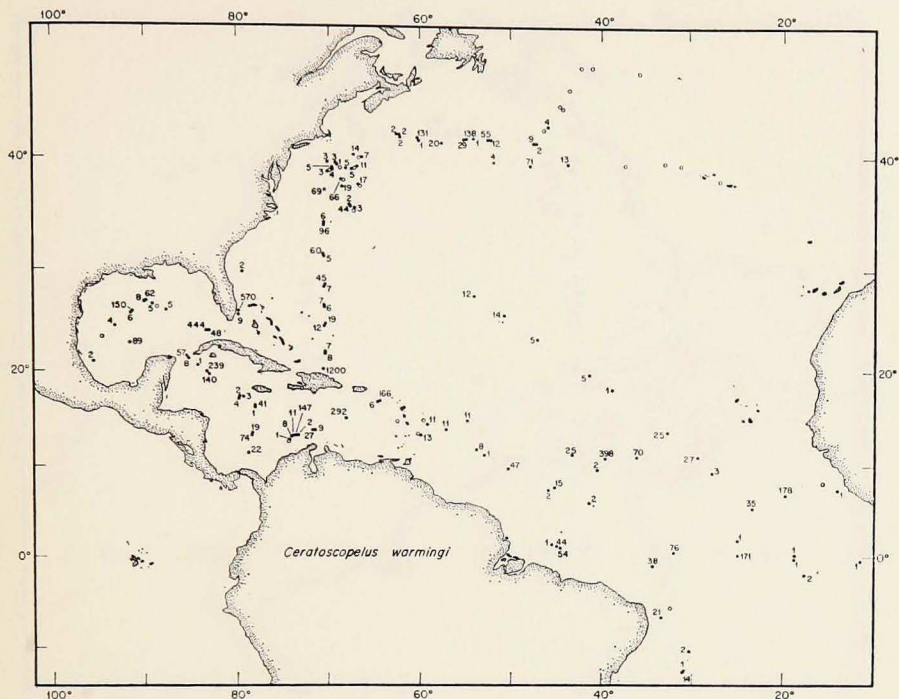
Figure 7. Distribution of *Ceratoscopelus warmingi*, showing the *broadly tropical* pattern. Compare this distribution with the distribution of its congener *C. maderensis* (Fig. 13).

for 14°C (Backus et al. 1965) as drawn by Schroeder (1963). It runs from the coast of Africa at about 20°N west-southwestward to the offing of British Guiana.

ix. The northwestern boundary of the South Atlantic Ocean counter-clockwise gyre located off Brazil. This gyre is more or less homologous with the Sargasso Sea in the North Atlantic. This boundary is set to follow the 15°C isotherm for 200 m. The choice of this isotherm for limiting the gyre is made on the advice of W. G. Metcalf (personal communication) and is drawn following Wüst and Defant (1936).

x. A boundary running south along the meridian 30°W between boundaries viii and ix. This boundary is imprecisely drawn for want of information (and so is shown by a broken line). It is meant to divide the equatorial Atlantic into eastern and western parts, the eastern part in the upper levels of the water column being somewhat cooler and fresher and having less dissolved oxygen than the western part. These differences are associated with upwelling and the resulting increase in productivity in the waters off the African coast. It is probable that the difference in productivity is ultimately responsible for the faunal differences noted. The boundary shown follows the chart of primary
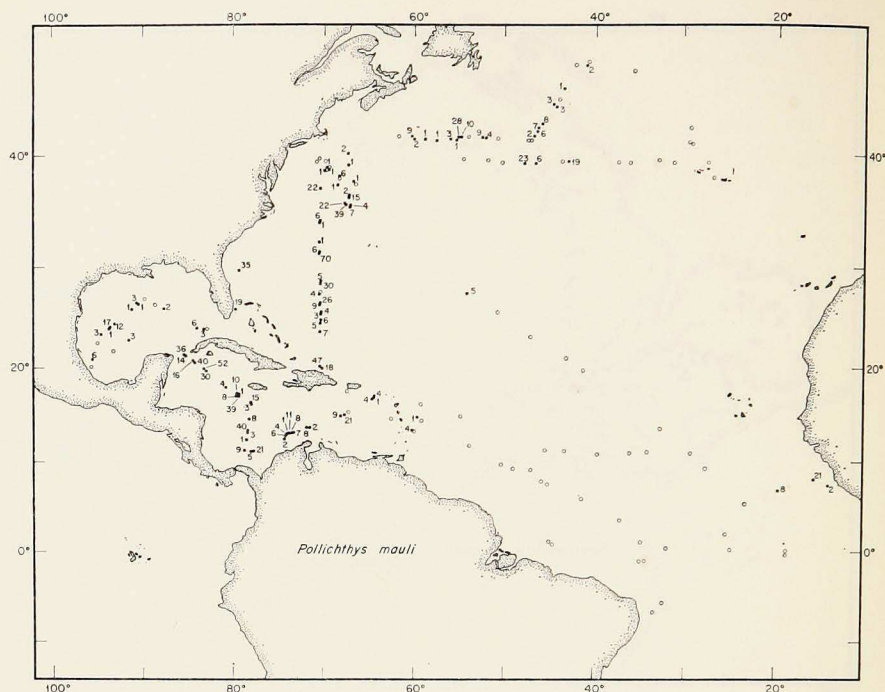
Figure 8. Distribution of *Pollichthys mauli*.

production drawn by Fleming and Laevastu (1956) as modified by Ebeling (1962).

Although all these boundaries are defined and drawn as lines, it must be understood that they are not only broad ones due to the great irregularities always found, but also shifting ones. Fig. 4 depicts an average situation, then, and a certain set of geographic coordinates may lie within one region on one occasion and within a second on another occasion.

Distribution Patterns. Figs. 6–17 are range maps exemplifying the North Atlantic distribution patterns noted so far. Each pattern results from the occurrence of species in a certain set of pelagic regions. The patterns noted and the assignment of species to them are based solely upon our own data. Seventy-eight species have been assigned a distribution pattern. Naturally, we are more confident of some of these assignments than of others. Therefore, we have used a question mark to distinguish those species about which we feel less sure. In the few cases in which published data have argued against an interpretation that we would have made from our own data, we have dropped the species in question from present consideration.

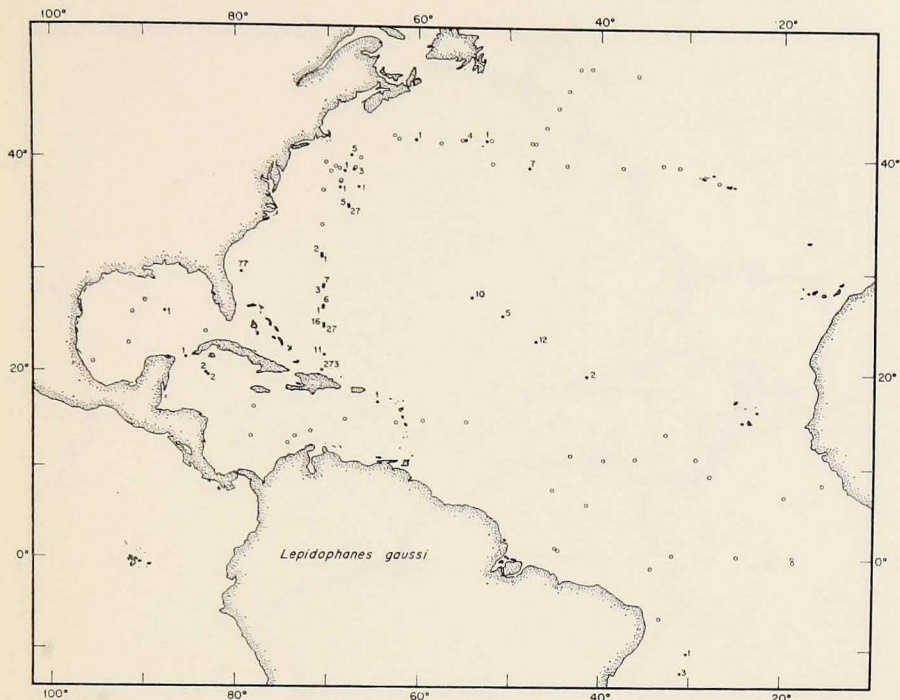A map showing the occurrence of a species is useful only if it shows the

Figure 9. Distribution of *Lepidophanes gaussi*, showing the *Sargasso Sea* pattern.

distribution of the effort leading to the taking of the species; that is, such a map not only must show where a species was taken, but also, as far as possible, show where it might have been taken but was not. Our maps have been prepared in the following way: for each species, the number of specimens taken has been plotted, collection by collection, on work sheets that show the depth and time of day of the collections (Fig. 1). From such plots the daytime and night-time depth limits of species as they occur in our collections have been established. Collections falling outside a species' depth limits have been considered everywhere inappropriate for taking that species, while collections falling inside a species' depth limits have been considered everywhere appropriate for taking a species even if specimens of that species were not actually caught in these collections. In Figs. 6–17, collections deemed appropriate for taking a species, but which actually contained none, are represented by open circles; collections that contained specimens are entered as dots, with the number of specimens taken entered alongside each dot. The hazard attached to this procedure is the possibility that a species may have different depth limits in different parts of the ocean. An example is found in the phenomenon of tropical submergence, whereby certain animals living in nearsurface waters in far-northern seas are found in the tropics deep in the water column at the
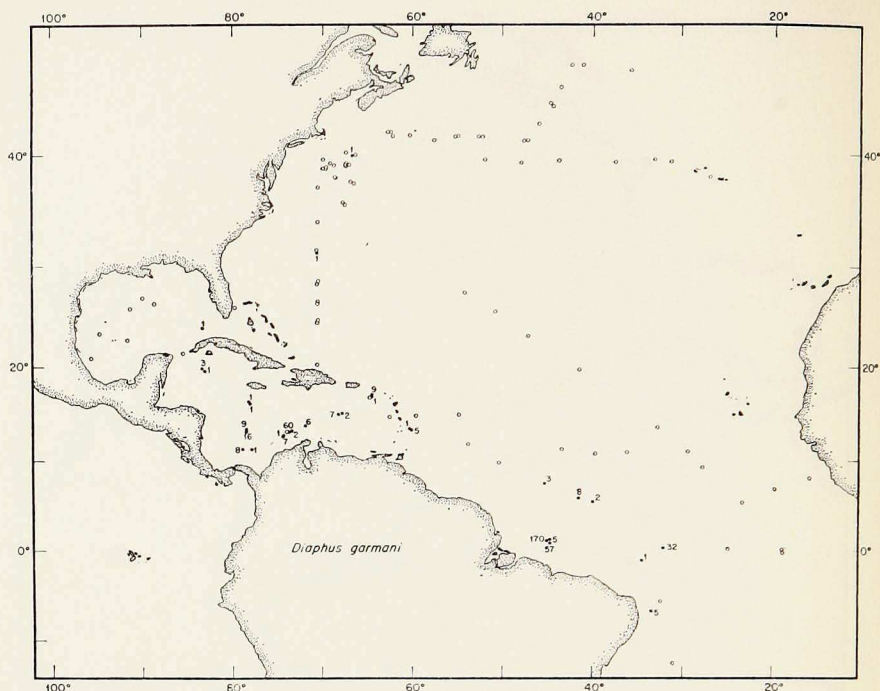
Figure 10. Distribution of *Diaphus garmani*, a species restricted to the Amazonian Region and Caribbean Sea.

level of the appropriate temperature. However, the mesopelagic fishes that we have sampled well are mainly diurnal vertical migrators that come into the epipelagial by night. We have noted only small changes in the vertical distribution of such species from one region of the ocean to another—changes insufficient to cause us to catch a species in one region but to miss it in another from want of sampling over a sufficiently wide range of depths. Fig. 5, for instance, shows that *Pollichthys mauli* was not simply overlooked in the Amazonian and Lesser Antillean regions through our failure to sample at the correct temperature.

The *tropical* distribution is exemplified by the distribution of *Gonostoma atlanticum* (Fig. 6). A *tropical* species is defined as one that regularly lives in the Guinean, Amazonian, and Lesser Antillean regions and in the Caribbean Sea and Gulf of Mexico. Such a species is mainly absent from the Northern and Southern Sargasso seas, although it can be found in small numbers in the northern part of the Northern Sargasso Sea, in the Slope Water Region, and even beyond the tail of the Grand Bank in the Eastern Gyre. It is presumed that such specimens are waifs, carried north to these places by the Gulf Stream. As a rule, a *tropical* species is more abundant in the Caribbean Sea than it is
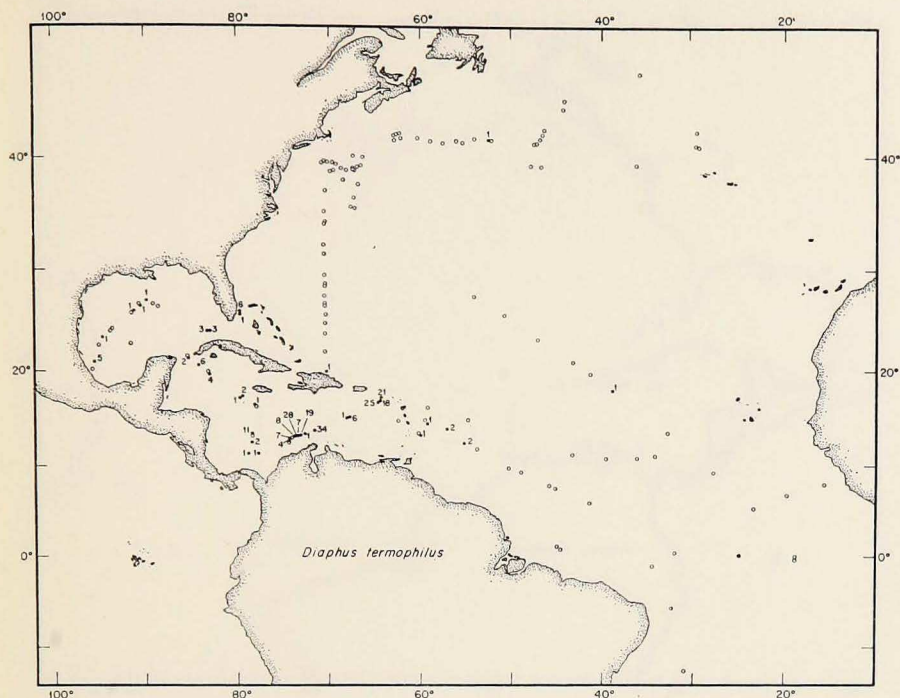
Figure 11. Distribution of *Diaphus termophilus*, a species restricted to the Caribbean Sea and Gulf of Mexico.

in the Gulf of Mexico. So far, 22 species have been assigned to the *tropical* pattern. These are the myctophids *Diaphus brachycephalus*, *D. dumerili*, *D. fragilis*, *D. lucidus*, *D. luetkeni*, *D. problematicus*, *D. splendidus*, *D. subtilis*, *Hygophum macrochir?*, *Lampanyctus alatus*, *Lampadena luminosa*, *Lepidophanes guentheri*, *L. supralateralis?*, *Myctophum affine*, *M. asperum*, and *M. obtusirostris*, the gonostomatids *Gonostoma atlanticum*, *G. elongatum?* and *Vinciguerria nimbaria?*, and the stomiatoids *Astronesthes richardsoni*, *Bathophilus pawneei*, and *Stomias affinis*.

The *broadly tropical* pattern is exemplified by the distribution of *Ceratoscopelus warmingi*[3] (Fig. 7). A *broadly tropical* species lives in the same regions where a tropical species lives but also occurs regularly in the Northern and Southern Sargasso seas and in the Slope Water Region. Small numbers are found just beyond the tail of the Grand Bank in the Eastern Gyre. As a rule, a *broadly tropical* species is more abundant in the Gulf of Mexico than it is in the Caribbean Sea (the converse being true for *tropical* species). To date, nine species have been assigned to the *broadly tropical* pattern. These are the

3. North Atlantic specimens of this species have generally been called *C. townsendi* (Eigenmann and Eigenmann). See Nafpaktitis and Nafpaktitis (1969).
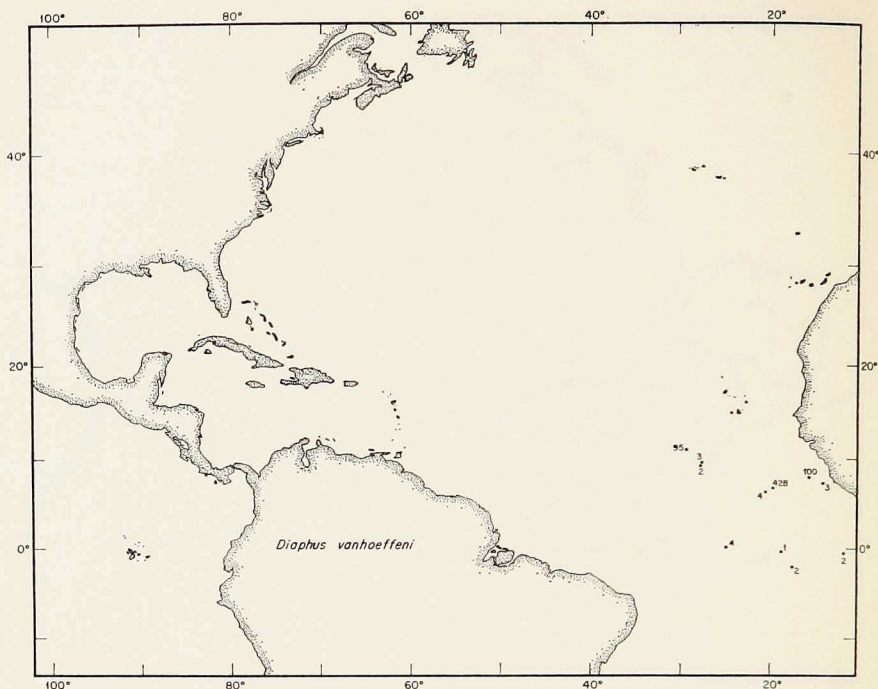
Figure 12. Captures of *Diaphus vanhoeffeni*, a species frequenting the North Atlantic only in the Guinean Region. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits for the species.

myctophids *Benthosema suborbitale, Centrobranchus nigroocellatus?, Ceratoscopelus warmingi, Diaphus mollis, Myctophum nitidulum,* and *Notoscopelus resplendens;* also *Argytopelecus sladeni?, Diplospinus multistriatus,* and *Lestidiops affinis?*

The gonostomatid *Pollichthys mauli* has an interesting range (Fig. 8). It is distributed according to the *broadly tropical* pattern except that, though present in the Guinean Region, it is wholly wanting in the Amazonian Region. We have also found *P. mauli* in the western South Atlantic, between about 23°S and the Subtropical Convergence in the offing of the Rio de la Plata. The range of *Coccorella atrata* may be similar to that of *P. mauli.*

Four other warm-water distribution patterns are evident, but none has had many species assigned to it. The range of *Lepidophanes gaussi* exemplifies the *Sargasso Sea* pattern (Fig. 9). Such a species mainly occurs in our Northern and Southern Sargasso Sea collections. It has also been found in meagre numbers in the northern part of the Caribbean Sea, into which Sargasso Sea water spills via the Windward Passage (Worthington 1959). It is probable, however, that none of the five species assigned to this pattern (the myctophids *Diaphus*
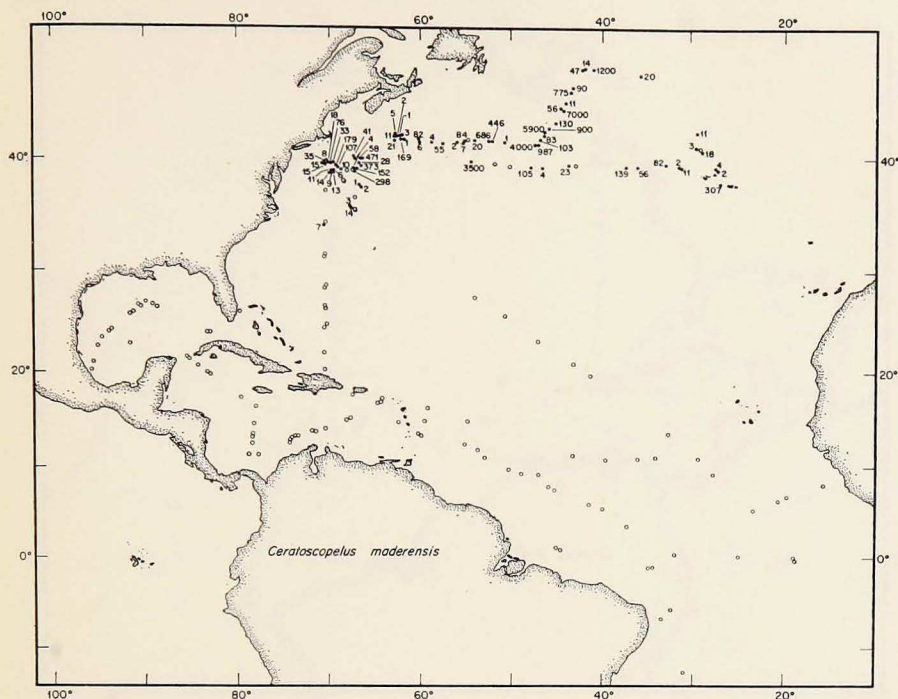
Figure 13. Distribution of *Ceratoscopelus maderensis*, showing the *northern* pattern in which the northern edge of the Gulf Stream forms the southern limit in the west.

effulgens and *Lepidophanes gaussi*, and the stomiatoids *Chauliodus danae*, *Eustomias obscurus?*, and *Idiacanthus fasciola?*) finds its eastern limit at the edge of the Sargasso Sea as here defined. *C. danae* and *L. gaussi*, for instance, are among a list of eight "commoner" species found at 30°N, 22°W (Harrisson 1967). It is possible that fishes having this distribution pattern are adapted for living in the central least-productive regions of the North Atlantic, of which the Sargasso Sea forms but a part. *Diaphus effulgens*, *C. danae*, and *L. gaussi* are also found in the South Atlantic Ocean in the unproductive gyre off central Brazil.

Diaphus garmani (Fig. 10) and *D. elucens* appear to be restricted to the Caribbean Sea and Amazonian Region. *Diaphus termophilus* (Fig. 11), *Astronesthes similis*, and *Cubiceps athenae* are found mainly in the Caribbean Sea and Gulf of Mexico. *Diaphus vanhoeffeni* (Fig. 12) and *Chauliodus schmidti* occur only in our collections from the Guinean Region.

The essentially warm-water species, then, number 45 and are distributed according to seven patterns.

Twenty-two species have northern ranges. It is obvious that the species included are distributed according to several patterns, but it is not possible to
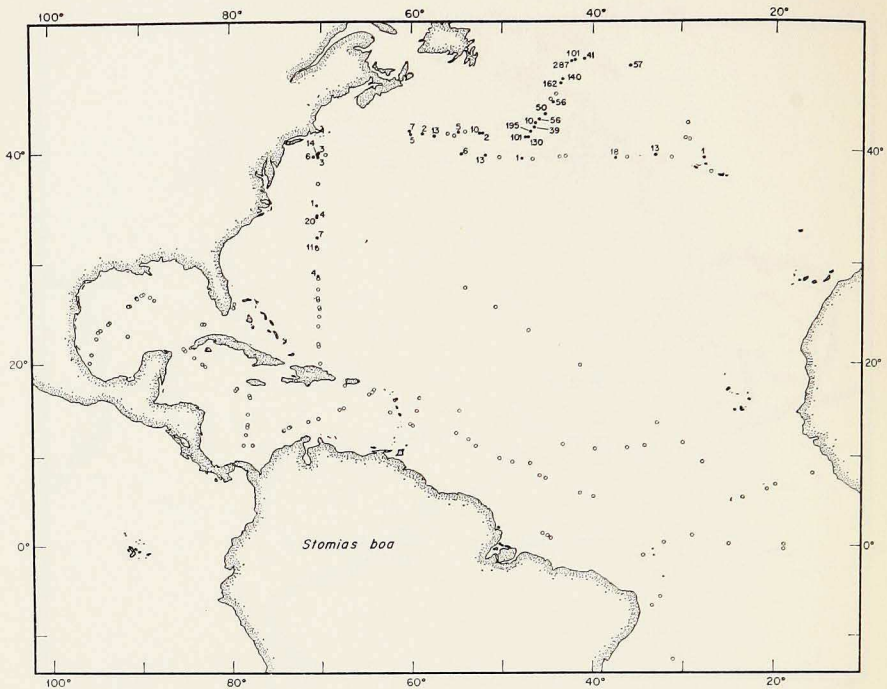
Figure 14. Distribution of *Stomias boa*, showing the *northern* pattern in which the area of the thermal fronts in the Sargasso Sea forms the southern limit in the west.

describe these patterns because so little is known about the northern and southern limits of these northern species in the eastern North Atlantic. All are widespread in European seas (Bolin 1959), and all, with two or three exceptions, are found in the Mediterranean Sea (Tåning 1918). These species can be tentatively arranged in three groups according to the southern limit of their ranges in the western North Atlantic.

One group, exemplified by *Ceratoscopelus maderensis* (Fig. 13), finds its southern limit at the Gulf Stream edge. This group includes the myctophids *Benthosema glaciale*, *Ceratoscopelus maderensis*, *Diaphus metopoclampus*, *Diaphus rafinesquei*, *Hierops arctica*, *Myctophum punctatum*, *Notoscopelus krøyeri*, and *Symbolophorus veranyi*, and the paralepidid *Notolepis rissoi*.

A second group finds its southern limit in the west at the boundary between Northern and Southern Sargasso seas. This group includes the myctophids *Lampadena chavesi?*, *Lampanyctus crocodilus*, *L. pusillus*, and *Lobianchia dofleini*, and the stomiatoids *Bathophilus metallicus* and *Stomias boa* (Fig. 14).

Species in the third group find their southern limit in the Gulf of Mexico although they are mainly absent from the Southern Sargasso Sea. The group includes the myctophids *Gonichthys coccoi?*, *Hygophum benoiti*, and *H. hygomi*,
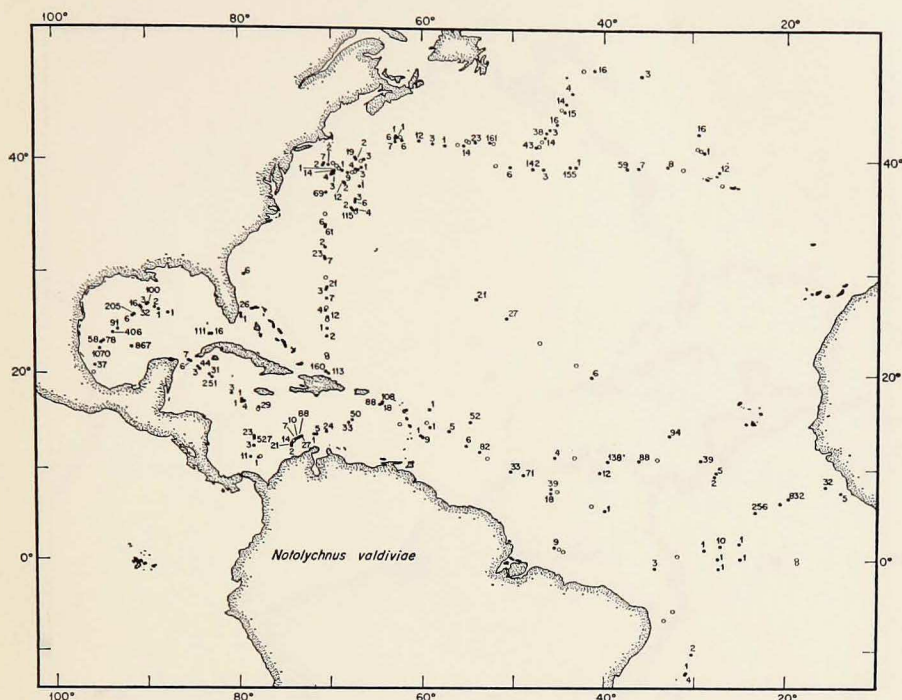
Figure 15. Distribution of *Notolychnus valdiviae*, a widespread species.

the gonostomatids *Maurolicus muelleri*, *Vinciguerria attenuata*, and *V. poweriae*, and the stomiatoid *Astronesthes niger?*

Species of the first group tend to be endemic to the North Atlantic, species of the second group tend to be biantitropical, and species of the third group tend to range across the equator in the eastern Atlantic into the southern hemisphere. Because species of the last group can be waifed into the Amazonian Region by the westward-flowing South Equatorial Current, it may appear that such species are absent in the North Atlantic only from the Caribbean and Southern Sargasso seas.

The distribution of *Notolychnus valdiviae* (Fig. 15) is representative of a group of seven widespread species that includes the myctophids *Diogenichthys atlanticus*, *Lobianchia gemellari*, and *Notolychnus valdiviae*, the gonostomatids *Bonapartia pedaliota*, *Ichthyococcus ovatus*, and *Valenciennellus tripunctulatus*, and the sternoptychid *Argyropelecus hemigymnus*. These species have been found wherever we have collected. It is clear, however, that they are not ubiquitous in the North Atlantic, for some, if not all, have northern or eastern limits. Furthermore, certain ones inhabit the Mediterranean Sea while others do not, so that the assignment of these species to two or more distribution patterns at some time in the future is assured.
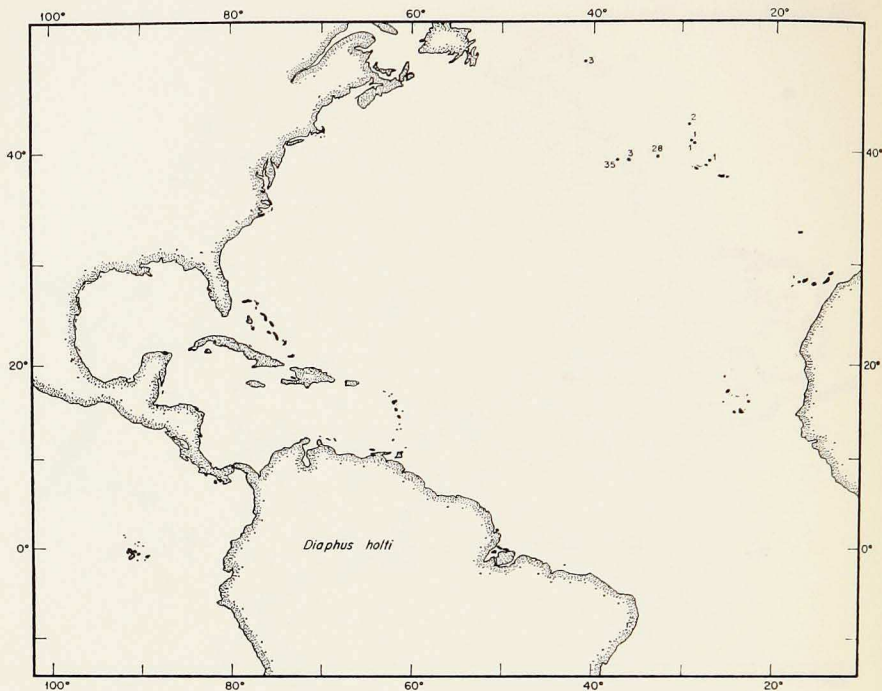
Figure 16. Captures of *Diaphus holti*, a species found only in our eastern collections. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits.

A few species occur only in our few eastern collections. We can say very little about their distribution. Several patterns are involved. *Diaphus holti* (Fig. 16), for instance, is principally an inhabitant of the northeastern Atlantic and ranges south along the west coast of Africa to about 5°N, but not apparently beyond (Nafpaktitis 1969). *Electrona rissoi* (Fig. 17), on the other hand, crosses the equator and is said to occur all along the west coast of Africa to the Cape of Good Hope (Bolin 1959). Other species occurring only in our eastern collections are *Gonostoma denudatum* and *Argyropelecus olfersi*.

Concluding Remarks. From the variety of overlapping distribution patterns, it follows that each pelagic region is faunally distinct with its characteristic assemblage of species whose numbers are in characteristic proportion, its characteristic diversity, and so on. A few inter-regional comparisons are presented in Tables I and II.

Tentatively, we can divide that portion of the North Atlantic with which we are familiar into a tropical part (Gulf of Mexico, Caribbean Sea, and Amazonian, Lesser Antillean, and Guinean regions) and a northern part
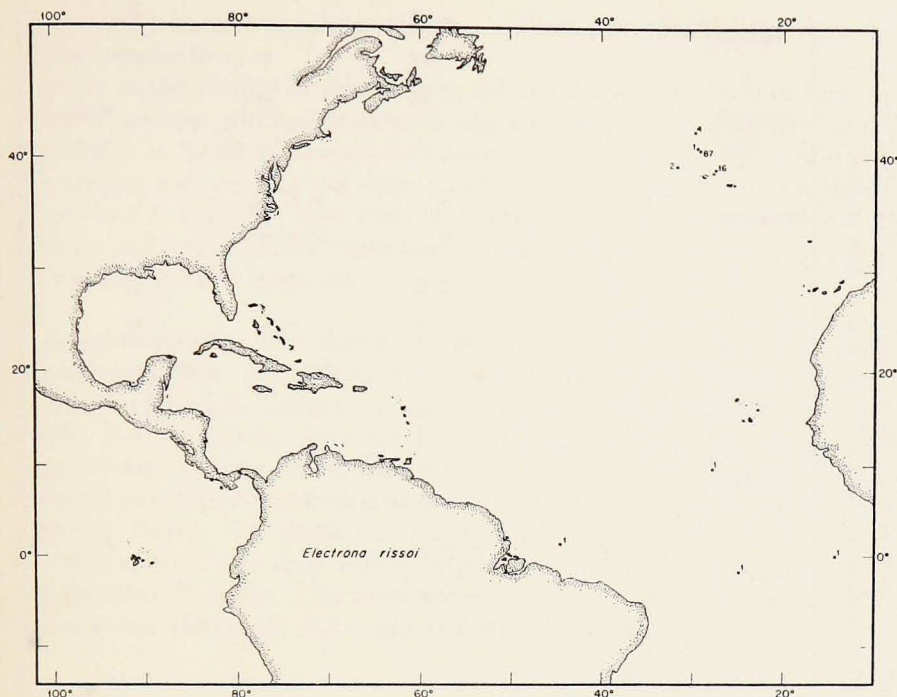
Figure 17. Captures of *Electrona rissoi*, another species found only in our eastern collections. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits.

(north of 35°N or 40°N), with the two parts separated by a wide transition region, the Sargasso Sea. The Sargasso Sea itself is divisible into a cooler and more productive northern part, having a mixture of northern and tropical

Table I. Some properties of shallow (< 200-m) night-time collections according to region of origin. The number in parentheses is the number of collections entering each sample.

Pelagic region	No. of species	Specimens per hour	cc per hour	Diversity index (H)
Labrador (4)	56	2804	687	.71
Slope Water (5)	87	378	74	2.67
Eastern Gyre (10)	70	380	61	1.48
Northern Sargasso Sea (13)	98	149	35	3.08
Southern Sargasso Sea (7)	55	42	15	2.62
Gulf of Mexico (8)	127	260	95	2.92
Caribbean Sea (20)	153	171	58	3.35
Lesser Antillean (6)	67	97	55	3.00
Amazonian (13)	91	223	72	2.86
Guinean (8)	101	485	–	2.65

Table II. Principal species in shallow (<200-m) night-time collections by pelagic region. The numbers in the first column under each region show the abundance rank within the region. The italic numbers in the second column under each region show the percentage of the total number of specimens in the region's collections that the species comprises. The species included are all of those having an abundance rank of five or less in any region.

Species	Pattern*	Labrador		Eastern Gyre		Slope Water		Northern Sargasso Sea		Southern Sargasso Sea		Gulf of Mexico		Caribbean Sea		Amazonian		Lesser Antillean		Guinean	
Benthosema glaciale	N 1	1	*82*	2	*10*	5	*5*														
Ceratoscopelus maderensis	N 1	2	*13*	1	*65*	2	*20*														
Lobianchia dofleini	N 2					1	*27*														
Lampanyctus pusillus	N 2	5	*.6*	3	*6*	3	*6*	4	*10*												
Stomias boa	N 2	3	*1*																		
Lampanyctus crocodilus	N 2	4	*.8*																		
Maurolicus muelleri	N 3			4	*5*																
Hygophum benoiti	N 3			5	*4*																
Diogenichthys atlanticus	W							1	*14*												
Ceratoscopelus warmingi	Bt							2	*13*	1	*57*			3	*11*	3	*11*			5	*5*
Notolychnus valdiviae	W							3	*12*	3	*9*	1	*19*	4	*10*			2	*13*	2	*14*
Pollichthys mauli	Sc							5	*6*	4	*3*										
Lepidophanes gaussi	SS									2	*15*										
Lampanyctus photonotus	?									5	*2*										
Benthosema suborbitale	Bt											3	*15*			5	*5*				
Diaphus dumerili	T													1	*12*	2	*11*				
Lepidophanes guentheri	T													2	*11*	1	*23*	1	*23*	3	*9*
Gonostoma elongatum	T ?					4	*5*											5	*6*		
Lampanyctus alatus	T											2	*16*			4	*5*				
Vinciguerria poweriae	N 3											4	*10*								
Melamphaes pumilus	?											5	*5*								
Vinciguerria nimbaria	T ?													5	*6*					1	*32*
Lampanyctus nobilis	?																	3	*8*		
Diaphus brachycephalus	T																	4	*6*		
Diaphus vanhoeffeni	G																			4	*6*

* N = Northern, W = Widespread, Bt = Broadly tropical, Sc = Special case, SS = Sargasso Sea, T = Tropical, G = Guinean. Question mark, when standing alone, indicates that it has not been possible to assign the species in question to a pattern; when following a pattern symbol, the assignment is questionable.

species, and a warmer and less productive southern part, in which a few mainly tropical species live.

So far as the ecology of species goes, the distribution pattern is of first importance, and the principal question is why a given species is distributed in the way that it is. So far as community ecology goes, the pelagic region is of first importance, and we may ask why a certain region supports the complex of species that it does. We hope that information about the distribution and life histories of North Atlantic mesopelagic organisms will some day be adequate for answering these questions.

REFERENCES

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, and D. L. SHORES
   1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. Mar. Biol., *3*: 87–106.

BACKUS, R. H., and J. B. HERSEY
   1956. Echo sounder observations of midwater nets and their towing cables. Deep-sea Res., *3*: 237–241.

BACKUS, R. H., G. W. MEAD, R. L. HAEDRICH, and A. W. EBELING
   1965. The mesopelagic fishes collected during Cruise 17 of the R/V CHAIN with a method for analyzing faunal transects. Bull. Mus. comp. Zool., *145*: 139–158.

BARTLETT, M. R., and R. L. HAEDRICH
   1968. Neuston nets and South Atlantic larval blue marlin (*Makaira nigricans*). Copeia, 1968 (3): 469–474.

BIERI, R. H.
   1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. Oceanogr., *4*: 1–28.

BOLIN, R. L.
   1959. Iniomi, Myctophidae from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. Rep. N. Atl. Deep-sea Exped. 1910, *4*, 2 (7): 1–45.

BRINTON, E.
   1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., *8*: 51–270.

CLARKE, G. L., and R. H. BACKUS
    1964. Interrelations between the vertical migration of deep scattering layers, bioluminesc-
        ence, and changes in daylight in the sea. Bull. Inst. océanogr. Monaco, *64* (1318):
        1–36.

EBELING, A. W.
    1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic
        fish genus *Melamphaes* Günther. Dana-Report, No. 58: 1–164.

EBELING, A. W., and W. H. WEED, III
    1963. Melamphaidae III. Systematics and distribution of the species in the bathypelagic
        fish genus *Scopelogadus* Vaillant. Dana-Report, No. 60: 1–58.

FAGER, E. W., and J. A. McGOWAN
    1963. Zooplankton species groups in the North Pacific. Science, *140* (3566): 453–460.

FLEMING, R. H., and TAIVO LAEVASTU
    1956. The influence of hydrographic conditions on the behavior of fish. FAO Fish. Bull.,
        9: 181–196.

GREY, MARION
    1964. Family Gonostomatidae, *In* Fishes of the western North Atlantic. Mem. Sears
        Found. Mar. Res.,*1* (4): 78–240.

HAFFNER, R. E.
    1952. Zoogeography of the bathypelagic fish, *Chauliodus*. Syst. Zool., *1*: 113–133.

HARRISSON, C. M. H.
    1967. On methods for sampling mesopelagic fishes. Symp. Zool. Soc. London, *19*: 71–126.

ISAACS, J. D., and L. W. KIDD
    1953. Isaacs-Kidd midwater trawl. Rep. Scripps Inst. Oceanogr., *53*–3: 1–21.

KATZ, E. J.
    1969. Further study of a front in the Sargasso Sea. Tellus, *21*: 259–269.

LAEVASTU, TAIVO
    1963. Evaluation of the sea. Rep. Hawaii Inst. Geophys., *42*.

McGOWAN, J. A.
    1960. The relationship of the distribution of the planktonic worm, *Poeobius meseres* Heath,
        to the water masses of the North Pacific. Deep-sea Res., *6*: 125–139.

NAFPAKTITIS, B. G.
    1969. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus*, in
        the North Atlantic. Dana-Report, No. 73: 1–131.

NAFPAKTITIS, B. G., and MARY NAFPAKTITIS
    1969. Lanternfishes (family Myctophidae) collected during cruises 3 and 6 of the R/V
        ANTON BRUUN in the Indian Ocean. Bull. Los Angeles Co. Mus., *5*: 1–79.

NEUMANN, GERHARD, and W. J. PIERSON, JR.
    1966. Principles of physical oceanography. Prentice-Hall, Inc., Englewood Cliffs. 545 pp.

PAXTON, J. R.
    1967. A distributional analysis for the lanternfishes (Family Myctophidae) of the San
        Pedro Basin, California. Copeia, 1967 (2): 422–440.

PEARCY, W. G., and R. M. LAURS
    1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-sea Res.,
        13: 153–165.

PICKFORD, GRACE
    1946. *Vampyroteuthis infernalis* Chun, an archaic dibranchiate cephalopod. I. Natural
    history and distribution. Dana-Report, No. 29: 1–40.

SCHROEDER, ELIZABETH H.
    1963. North Atlantic temperatures at a depth of 200 meters. Serial Atlas Mar. Environ.,
    Folio 2.

TÅNING, A. V.
    1918. Mediterranean Scopelidae. Rep. Danish oceanogr. Exped. 1908–1910, *2* (7): 1–154.

VOORHIS, A. D., and J. B. HERSEY
    1964. Oceanic thermal fronts in the Sargasso Sea. J. geophys. Res., *69*: 3809–3814.

WORTHINGTON, L. V.
    1959. The 18° water in the Sargasso Sea. Deep-sea Res., *5*: 297–305.

    1962. Evidence for a two-gyre circulation system in the North Atlantic. Deep-sea Res.,
    9: 51–67.

    1964. Anomalous conditions in the Slope Water area in 1959. J. Fish. Res. Bd. Canada,
    21: 327–333.

WÜST, GEORG, and ALBERT DEFANT
    1936. Schichtung und Zirkulation des Atlantischen Ozeans. Schnitte und Karten von
    Temperatur, Salzgehalt und Dichte. Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor'
    1925–1927, Bd. VI, Atlas.