

DISTRIBUTION PATTERNS OF OCEANIC FISHES IN THE ATLANTIC OCEAN

Selected problems

by Gerhard KREFFT

ABSTRACT

Some problems in the geographical distribution of oceanic midwater fishes in the Atlantic Ocean are discussed.

Remarkable differences were observed in the latitudinal distribution of mesopelagic fish species in the North Atlantic Ocean. These can be related to the oceanic circulation. The Gulf Stream system gives rise to a discontinuity in the position of the oceanic Polar Front. This front, a sharp boundary between subpolar and subtropical waters, follows the northern edge of the Gulf Stream in the western part of the ocean. East of about 25° W the Polar Front becomes weak and untraceable. Relatively warm, high-saline water of the North Atlantic Current flows north and northeastward by the spreading of the Mediterranean Intermediate Water. Due to the peculiarities of the circulation, secondary Polar Fronts are built up at the borders of the Norwegian and the Greenland Seas. The discontinuity of the Polar Front results in a broad zonal range extension of midwater fishes to the north and northeastward. An analysis of the fishes captured during the International Overflow '73 Expedition of ICES confirms the well-known earlier observations of an unhampered northward drift of many temperate and subtropical species up to the secondary Polar Fronts.

The waters of the Atlantic sector of the Antarctic Ocean harbour a faunal community of midwater fishes quite distinct from communities found to the north of the Subtropical Convergence. PARIN *et al.* (1974) subdivide the fauna into a subantarctic or notalian, and an antarctic group. This classification is rechecked in the light of the recent « Walther Herwig » cruises to the area. Four distribution patterns at least are described for the species of the Notalian Zone. The existence of a genuine Antarctic midwater fish fauna remains doubtful at present.

The distribution patterns of deep-living mesopelagic fishes rarely taken by smaller gear are compared with those of the common diurnally migrating species. A tendency of the constantly deep-living fishes to enlarge their areas is observed. Bathypelagic species may belong either to the « Widespread Pattern » or to specialized patterns, which are interpreted as niches acquired or enforced by competition. Such patterns are known as yet in some alepocephaloid fishes only.

INTRODUCTION

Pelagic zoogeography has been advanced mainly through zooplankton studies, especially in the Pacific Ocean, made by scientists and students in the USSR, the United States and elsewhere. Many of these studies included the smaller types of mesopelagic fishes, considering them as belonging to the plankton rather than to the nekton; others dealt exclusively with fishes.

Suffice it here to mention only a few workers who have summarized the results of such investigations, e.g. BEKLEMISHEV and PARIN (1960), BOGOROV (1958), MCGOWAN (1971, 1974), and for the epipelagic, PARIN (1970).

Studies comparable to those in the Pacific Ocean are few and full of gaps in the geographic coverage. Many of them have been restricted to selected taxa or groups of taxa, others to limited areas. Attempts to develop an ichthyo-geographical picture of the whole Atlantic Ocean have so far been made only for the epipelagic (PARIN, 1970). BACKUS *et al.* (1970) reviewed the distribution of mesopelagic fishes in the equatorial and western North Atlantic Ocean, resulting in the recognition of six pelagic faunal areas comprising 11 types of distribution patterns. KREFFT (1974) investigated the distribution patterns of a number of mesopelagic species collected during the «Walther Herwig» expeditions to South America 1966-1971. He distinguished 13 patterns along the transects of the «Walther Herwig», most of which correspond closely to the framework of patterns found by the BACKUS group. Likewise in 1974 PARIN *et al.* published a paper on midwater fishes of the western South Atlantic, recognising 5 «typological groups» arranged according to the zonal distribution of these fishes. At present a number of papers dealing with the horizontal distribution of midwater fishes, exemplified mainly by the lanternfishes of the family *Myctophidae* are either in press or in preparation by BACKUS and his colleagues. Another report dealing with the taxonomy and distribution of the myctophids collected during the «Walther Herwig» and «Anton Dohrn» cruises in the Atlantic Ocean and the Atlantic sector of the Southern Ocean is being prepared by HULLEY.

BACKUS *et al.* (1970) suggest that the currently popular hypothesis of a more or less direct boundary effect of the water masses as defined by their temperature-salinity relationships cannot explain sufficiently the highly complex distribution patterns in the Atlantic Ocean, although the ranges of midwater fishes in general correspond rather well to the superficial distribution of the water masses. Other parameters, e.g. light intensity, oxygen concentration, water density and the productivity providing sufficient food of the «right» type, obviously play an important part, as discussed by KREFFT (1974) and by BADCOCK and MERRETT (1976). PARIN *et al.* (1974) point to the importance of intraspecific parameters, e.g. expatriation, the drift of parts of the population out of the reproductive area with currents. Such expatriates may or may be not lost for the breeding stock of a species depending on their ability to return to their spawning grounds. These authors therefore postulate careful investigations concerning the structure of a distribution pattern, i.e. its subdivision into spawning grounds, areas only visited during feeding migrations and sterile zones of expatriation.

Because most of the numerous research cruises had, and still have, to use small types of fishing gear, such zoogeographical investigations concentrate on species easily obtained by such gear, which, like any gear, is very selective. Nets of the size of a 10-foot Isaacs-Kidd-Midwater Trawl or an RMT 8 have a rather limited effectiveness in capturing larger and speedier fish; moreover, they must be towed many hours in greater depths where the numbers of fishes often decrease. We will not discuss here the various factors influencing the biases inevitable in using any type of fishing gear. Commercial fisheries, however, have shown conclusively a direct positive dependency of catch size on size of gear. Large nets not only capture more specimens but also larger ones. The number of species normally also increases with increasing net size. On the other hand, pygmy species such as most of the *Cyclothone* species, the myctophids *Ceratobranchius*, *Diogenichthys* and *Notolychnus*, and the early stages of many groups are heavily underrepresented in commercial trawl catches. A sampling programme ideally should be worked with a variety of different gear, but on most cruises shortage of time and personnel will not allow such a strategy.

The Institut für Seefischerei of the Federal Fisheries Research Board in Hamburg is one of the very few institutions of its kind employing a group of fish taxonomists in its staff. Making use of the two large research vessels of the Board, built as stern trawlers, we chose the large pelagic trawls used in the commercial herring fisheries for sampling the midwater fauna. Our standard gear became the Engel trawl of 1600 meshes circumference. When, in 1964, the exploration of the fisheries potential in various parts of the Atlantic Ocean began, we started a sampling programme of the oceanic nekton for taxonomic and zoogeographic purposes. Using at the beginning a 10' IKMT, we learned very soon from a few experimental hauls with the

then newly-designed Engel trawl that this gear could provide much more satisfactory results than the smaller types of gear. Since then, we have used Engel trawls exclusively for our transects. In addition, however, we made use of neuston nets on several cruises, and during our recent Antarctic expedition a group of scientists of the University at Kiel repeated all of our trawl stations by hauls with an RMT 1-8. The Engel trawl stations worked by us in 1966, 1968, 1971, 1973, 1974 and 1975/76 are shown in figure 1. In 1966, on the passage to Argentina,

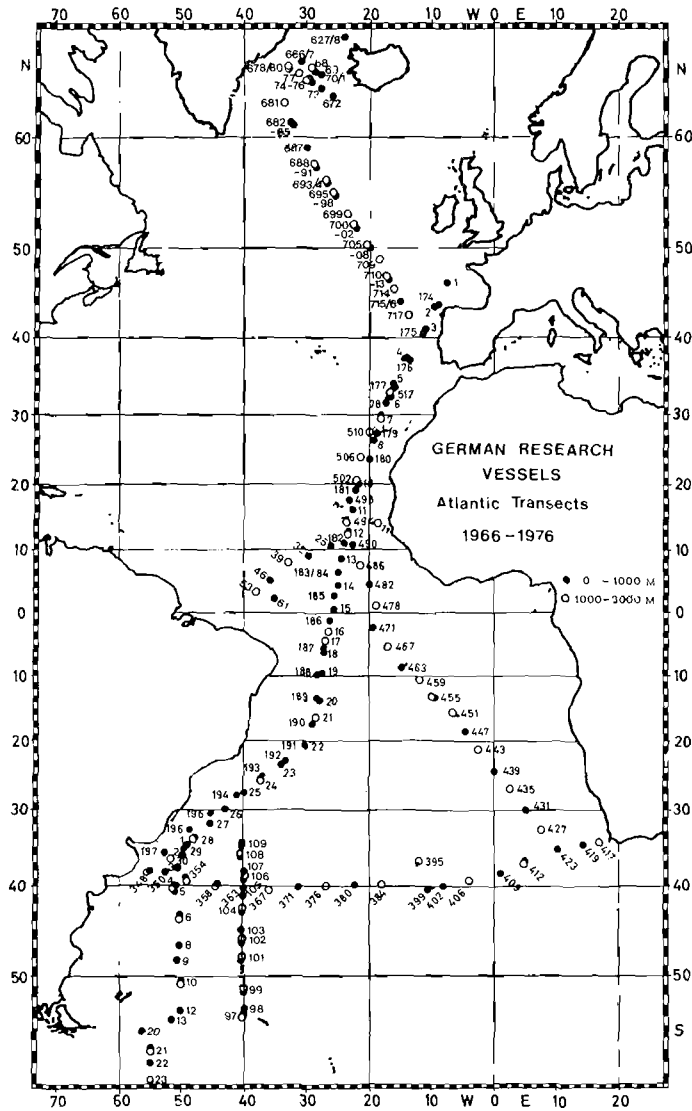


FIGURE 1

we made step hauls every night in depths ranging from about 850 to 50 meters. When repeating the transect in 1968 we changed to separate hauls fishing at depths selected according to the various scattering layers shown on the screen of the echo sounder, beginning with the shallowest chosen depth layer. Every night three hauls were executed in the layers less than 1 000 meters or a single deep haul at about 2 000 meters depth. The shallower hauls were controlled by using the «netzsonde». The depth of the deep hauls was measured by using a time-depth recorder. Up to 1971, aboard the first «Walther Herwig», the process of hauling

back the gear from great depths had to be interrupted at depths of 1000 and 500 meters in order to cool the trawl winch. This led to a rather bad contamination of the deep hauls by shallower-living species entering the net during the twenty-minute stops. Since 1973, using the «Walther Herwig II», we have been able to haul back the gear very speedily and without any break. Horizontal fishing in the selected layers ranged between 15 minutes in shallow hauls and 1 hour in deep hauls; the towing speed was 2,5 to 3,5 knots. «Walther Herwig I» fished to a maximum depth of 2 100 meters, «Walther Herwig II» to 3 100 meters.

Besides the stations shown in figure 1, information was gained from quite a number of Engel trawl hauls carried out during cruises that were exploring commercial aspects. These stations are omitted in figure 1, but some of them are shown on some of the following maps; in several cases additional information from published data is also included.

For the reasons already mentioned, I take this opportunity to discuss here the following topics:

- 1) the distribution patterns of mesopelagic fishes in the European parts of the North Atlantic Ocean,
- 2) those observed in the South Atlantic Ocean in, and south of, the Subtropical Convergence,
- 3) types of distribution of some deep-mesopelagic and bathypelagic species.

1) Distribution patterns of mesopelagic fishes in the European parts of the North Atlantic Ocean.

The system of distribution patterns worked out by BACKUS *et al.* (1970) for the midwater fishes inhabiting the equatorial and western North Atlantic Ocean consists of about a dozen patterns allotted to six pelagic regions. These regions are delimited by at least ten physical boundaries. The authors stressed the fact, that only very few species are restricted to a single region, and that the observed patterns «result mainly from the occupancy of various combinations of regions by species». In a forthcoming paper dealing with the zoogeography of the Atlantic myctophids these authors will proceed to a more elaborate system of seven zoogeographic regions encompassing 20 faunal provinces. The area south of the South Atlantic Subtropical Convergence is excluded by them, because the fish fauna beyond the convergence is considered as a part of a worldwide Southern Ocean fauna.

Naturally, the Atlantic Ocean could not be covered by the ships of the Woods Hole Oceanographic Institution with an evenly spaced net of stations. The authors therefore point to a number of incomplete or unsatisfactory parts of their system of faunal provinces.

I will try to deal here with one of the still somewhat problematical areas, viz. the eastern North Atlantic, the subdivision of which is still unsatisfactory.

In a previous publication (KREFFT, 1974) I distinguished two distribution patterns, the boreal and the temperate-subtropical, within the group of northern-temperate midwater fishes, fixing thereby their southern, but not their northern boundaries. It has been known for a long time, that the northern boundaries of many pelagic and archibenthal warm water species differ considerably in the eastern and western parts of the Atlantic Ocean. Such species in the western part of the ocean have their northern boundaries somewhere between about 35° and 52° N, i.e. either at the «boundary between the Slope Water to the north and the Gulf Stream and northern Sargasso Sea to the south», or «between the Labrador-Coastal Water to the north and the Slope Water and Eastern Gyre to the south» (BACKUS *et al.*, 1970). The same species range much farther northward in the eastern half of the ocean. Many of them have their northern boundaries south or west of Iceland, at about 65° N. The reason for these differences lies in the oceanic circulation. In the western North Atlantic the Polar Front «separates waters with different contents of oxygen and nutrients» (DIETRICH, 1964). It represents the boundary between cold, low-saline subpolar water and warm, high-saline subtropical water. Thus the Polar Front acts as a very sharp faunal boundary separating the Slope Water region from the Labrador region. East of about 25° or 20° W, depending on seasonal changes, the Polar Front becomes weak and untraceable, and ceases to act any more as a faunal barrier. Here, Mediterranean

Intermediate Water penetrates north- and northeastward along the western slope of Europe to the south of Iceland and the Denmark Strait, carried by the branches of the North Atlantic Current. In the eastern North Atlantic, therefore, a corresponding boundary between cold subpolar

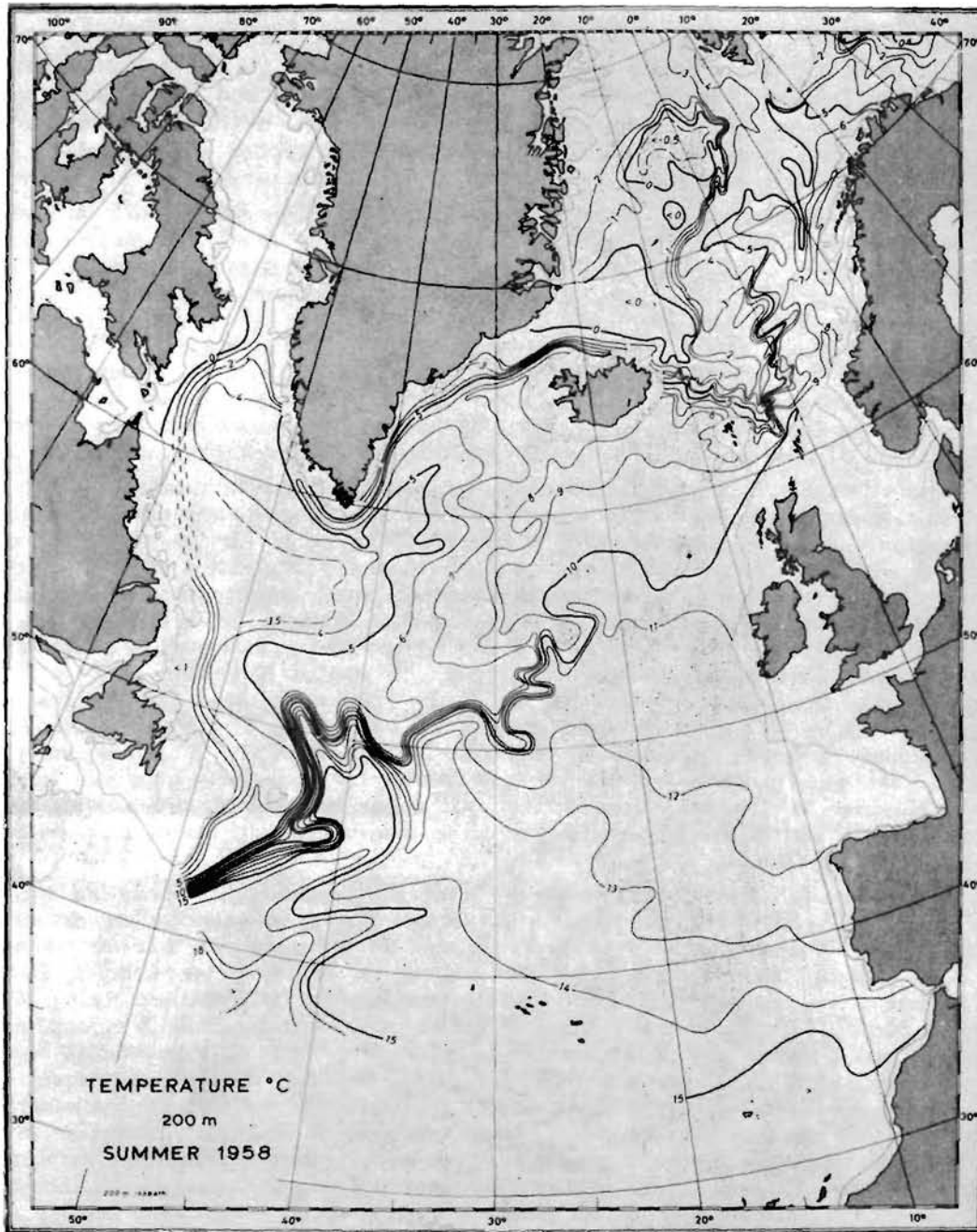


FIGURE 2

and warm Atlantic water, and between the subarctic and north-temperate faunas is built up by the secondary Polar Fronts in the Norwegian and Greenland Seas. The 200 m-isotherm for 5° C coinciding with the western and southern slopes of the Iceland-Faroe Ridge and the Iceland-Greenland Ridge marks the boundary very well (fig. 2).

It must be stressed that, obviously, there are no oceanic midwater fishes living exclusively in arctic or subarctic waters of the eastern North Atlantic, except for three benthopelagic abyssal species, which seem restricted to the cold seas beyond the Polar Fronts. These are the liparid species *Careproctus reinhardti*, *Paraliparis bathybius* and *Rhodichthys regina*.

A small number of midwater fish species, growing to a comparatively large size, have far ranging feeding migrations during the summer months beyond the Polar Front. *Alepisaurus ferox*, *Anotopterus pharao*, *Lampris guttatus*, *Trachipterus arcticus*, and *Centrolophus niger* can be mentioned. None of these have their spawning grounds in subarctic waters, but in subtropical or temperate areas. All of them, probably with the exception of *Trachipterus arcticus*, which is a north temperate-subtropical fish, belong to the bitemperate-subtropical pattern.

The number of species of the « smaller types » of mesopelagic fishes which immigrate into subarctic waters of the North Atlantic Ocean is also surprisingly small. The various records of G. JONSSON (1968, 1970, 1972, 1973 and 1975) provide a good survey of the distribution of midwater fishes around Iceland. To the north and northwest of Iceland only the following species have been observed: *Maurolicus muelleri* (N, NW), *Normichthys operosus* (NW), *Benthoosema glaciale* (NW), *Protomyctophum antarcticum* (NW), *Notoscopelus kroeyeri* (NW), *Paralepis atlantica* (NW), and *Nemichthys scolopaceus* (NW). East of Iceland *Stomias boa ferox*, *Notoscopelus kroeyeri* and *Notolepis rissoi* have been found. Taking again the spawning area as the decisive criterion for their allotment to a distribution pattern, we can exclude from a Boreoartic Pattern almost all of these species, leaving only the three myctophid species on the list.

The Polar Front(s) limits the ranges of numerous meso- and bathypelagic species to the north and east. According to the « fertile » parts of their ranges, north-temperate or boreal, north-temperate-subtropical and bitemperate patterns can be distinguished for the ichthyofauna of the eastern North Atlantic. During the International Overflow '73 Expedition three transects were run by the « Walther Herwig II » crossing the Denmark Strait between eastern Greenland and Iceland, followed by an oblique transect running southeastward from South Greenland to Lisbon. The secondary Polar Front between Greenland and Iceland was passed over by two mesopelagic fishes only, *Notolepis rissoi* and *Benthoosema glaciale*; 41 species had their northern boundary just south of this front. Between 60° and 55° N 21 species appeared for the first time in the hauls, followed by 27 species between latitudes 55° and 50° N. Finally, 17 species had their northern boundary between latitudes 50° and 40° N. Unfortunately, a precise analysis and allotment to distribution patterns has not yet been carried out; too many gaps still exist in our knowledge. However, it should be stressed, that, within the bathypelagic group, widespread and almost cosmopolitan species are best represented. The distribution patterns of most bathypelagic fishes are not very well understood.

The mesopelagic fishes making up about 40 % of the species collected during the pelagic sections of the « Overflow '73 Expedition » present a variety of distribution patterns. The Boreoartic Pattern is shown only by the myctophids *Protomyctophum arcticum*, *Benthoosema glaciale* and *Notoscopelus kroeyeri*, the Boreal Pattern by *Nansenia groenlandica*, *Bathylagus euryops* (?), *Argyropelecus olfersi* (probably bitemperate outside the Atlantic Ocean), *Paralepis coregonoides borealis*, *Myctophum punctatum* and *Lampanyctus crocodilus*. A group of seven species seems to represent the North-Temperate-Subtropical Pattern, viz. *Stomias boa ferox*, *Rhadinesthes decimus*, *Symbolophorus veranyi*, *Lobianchia dofleini*, *Diaphus rafinesquei*, *Ceratoscopelus maderensis*, and *Trachipterus arcticus* (?). Biantitropical patterns are allotted to the largest group of 16 species: *Derichthys serpentinus*, *Maurolicus muelleri*, *Chauliodus sloani* (?), *Borostomias antarcticus*, *Neonesthes capensis*, *Trigonolampa miriceps*, *Paralepis atlantica*, *Electrona rissoi*, *Diaphus effulgens*, *D. holti*, *D. metopoclampus*, *Lampadena speculigera*, *Lampanyctus ater*, *L. intricarius*, *L. macdonaldi*, and *L. pusillus*. This group is a somewhat heterogenous one consisting of bitemperate as well as bisubtropical species. Finally, a group of widespread species must be mentioned inhabiting temperate, subtropical and even tropical parts of the oceans. Species belonging to this group are, e.g. *Serrivomer beani*, *Nemichthys scolopaceus*, *Argyropelecus hemigymnus*, *Melanostomias spilorrhynchus*, *Notolepis rissoi*, *Lestidiops affinis*, *Diretmus argenteus*, *Howella brodiei*, *Chiasmodon niger*, and *Pseudoscopelus altipinnis*, to enumerate only the most important of them.

As the review shows, the temperate waters of the eastern part of the North Atlantic Ocean harbour a fairly mixed midwater fish fauna. Subarctic-temperate, boreal and subtropical elements merge evenly, almost unbroken by any gaps.

2) Some remarks on the midwater fish fauna of the South Atlantic Ocean south of 35°S.

Previously KREFFT (1974) assigned the oceanic midwater fishes of the South Atlantic Ocean living in and beyond the Subtropical Convergence to four basic patterns:

- a) the Convergence Pattern,
- b) the Westwind Drift Pattern,
- c) the Broadly Antarctic Pattern,
- d) the Bipolar Pattern.

The basis for these assignments were the fishes obtained in 1971 during the transect from Mar del Plata to Cape Town, running for the most part within the area of the South Atlantic Subtropical Convergence. The allotment of the species to the four patterns was carried out according to the then existing literature, since we had no or almost no material from the waters south of the convergence.

In the same year PARIN *et al.* (1974) published their important paper on midwater fishes of the southwestern Atlantic Ocean. According to an «evident zonal distribution» of the fishes obtained by the 11th cruise of the «Akademic Kurchatov» these authors assigned to them 5 distribution patterns:

- a) Antarctic,
- b) Subantarctic or Notalian,
- c) Peripheral Central or Subtropical,
- d) Central,
- e) Equatorial.

We shall consider here only the first two patterns, i.e. the Antarctic Pattern, exhibited by those fishes living and propagating south of the Antarctic Convergence, and the Subantarctic Pattern, shown by species living mainly and having their spawning places in the waters between the Antarctic and the Subtropical Convergences. The collections obtained by us during the Antarctic Expedition of the «Walther Herwig» in 1975/76 enabled us to reconsider the relevant questions.

The faunal situation in the western South Atlantic resembles to a certain degree that of the eastern North Atlantic, as there is a remarkable mixture of subtropical, temperate and subpolar species in the near-shore waters. This is due to the hydrographic conditions. Warm water of the Brazil Current transports subtropical species southward to about 40° S, whereas subantarctic species are carried northward by the Falkland Current up to about 35° S. At a depth of about 1 000 m the Antarctic Intermediate Water covers the slope of Brazil even to Cabo Frio at 22° S. Here we found many demersal and benthopelagic species of subantarctic origin in bottom trawl hauls in 1968.

In the upper 500 meters or so this transitional zone of mixed water is meridionally restricted to the vicinity of the South American Continent. This has been stressed by PARIN *et al.* (1974). In the open ocean subtropical and subpolar waters and faunal elements are kept apart very efficiently by the South Atlantic Subtropical Convergence area, a belt of variable breadth and seasonally changing position that stretches around the globe between about 35 and 40° S.

A very important difference between the North Atlantic and the Atlantic sector of the Southern Ocean exists in the formation of water masses. The Subantarctic Water Mass so characteristic for the area between Subtropical and Antarctic Convergences has no counterpart in the North Atlantic, Subarctic Water closely corresponding to the Subantarctic Water being formed in the North Pacific Ocean only. Therefore, the «Subpolar» Water of DIETRICH, found to the north of the Polar Front in the North Atlantic Ocean better corresponds to the

Antarctic Water than to the Subantarctic Water. Moreover, the Polar Front of the North Atlantic corresponds closely to the Antarctic Convergence, both being the dividing line between thermo- and psychrosphere at the surface of the sea. For that reason no peculiar subarctic midwater fauna could originate in the North Atlantic Ocean, and the relatively small number of north-temperate fishes, intermingled with subtropical elements, ranges northward just to the Polar Front.

In the Southern Ocean, on the other hand, a speciose circumglobal midwater fauna has originated in the Subantarctic Water Mass. However, there are indications that this fauna cannot be looked at as homogenous in its ecological valency. PARIN *et al.* (1974) were aware of a certain heterogeneity, observing that a number of species prevail or are confined even in the northernmost outskirts of the area. A preliminary analysis of the recent «Walther Herwig» catches strengthens the arguments for such a heterogeneity. Moreover, the existence of a strictly Antarctic midwater fauna must be questioned again, when we exclude at least the nototheniiform fishes, zoarcids and liparids. Ten species were assigned to the Antarctic Pattern by PARIN *et al.* Postulating that a strictly Antarctic species would be expected to have its spawning area south of the Antarctic Convergence, some species must be removed from the list. *Bathylagus antarcticus*, *Notolepis? coatsi* and *Benthalbella elongata*, the latter referred with a question mark to the Antarctic Pattern by PARIN *et al.* (1974), were found by us either in near-spawning condition or as postlarval stages inside the subantarctic zone. Unfortunately, the identification of *Notolepis coatsi* remains doubtful at present. Two closely related sympatric species were taken in fair numbers by the «Walther Herwig», both of which fit the original description of *N. coatsi* quite well. Since the single type specimen of DOLLO's species is in very poor condition, a decision which one of the two species actually represents *coatsi* cannot yet be given (A. POST, personal communication). No differences exist in the distribution patterns of *Benthalbella macropinna* and *B. elongata*. This appears from a comparison of fig. 21 and 28 in JOHNSON's revision of the scopelarchids (1974) as well as from our own captures. Moreover, the admittedly few known larval stages of both species were all found only in subantarctic waters.

A final answer to the question of the existence of a strictly Antarctic midwater fauna cannot be given here, before an evaluation of the distribution patterns of the most important southern myctophids will be presented by P.A. HULLEY, of Cape Town, in near future. Moreover, material collected during legs 2 and 3 of the Antarctic expedition in higher latitudes could not be studied up in time.

38 species have been assigned to the Subantarctic Pattern by PARIN *et al.* (1974). In my opinion their list represents a somewhat artificial grouping of species, representing at least three different patterns, although all of these species occur in subantarctic waters.

First, a group of bitemperate species certainly should be removed from the list. These are *Bathylagus euryops*, *Borostomias antarcticus*, *Lampanyctus intricarius*, and *L. macdonaldi*, all of which are also found in the North Atlantic Ocean.

A second group of species is plainly restricted to the mixed waters of the Subtropical Convergence and the northernmost fringe of the subantarctic zone. The following species listed by PARIN *et al.* as subantarctic elements fit better the «Convergence Pattern»: *Normichthys yahganorum* (fig. 9), *Diplophos rebaini*, *Bathophilus ater*, *Photonectes munificus*, *Astronesthes boulengeri* (fig. 3), *Hygophum hanseni*, *Diaphus ostenfeldi*, *Lampadena dea*, probably *L. notialis* and *Lampanyctus australis*. In addition, a number of species not mentioned by PARIN *et al.* (1974) belong to the group, viz. *Astronesthes psychrolutes* (fig. 3), *Opostomias micripnus* (fig. 3), *Eustomias trewavasae*, and *Scopelarchoides krefftii*, also the notosudids *Luciosudis normani*, *Scopelosaurus ahlstromi* and *S. meadi*.

Recent catches during the Antarctic Expedition of R/V «Walther Herwig» seem to throw some more light on the rather complex distributional relations of the southern notosudids. Just metamorphosed adolescents of the three species mentioned and of *Scopelosaurus hamiltoni* were found, as in earlier cruises, inside the Subtropical Convergence area. During growth these fishes penetrate farther into the subantarctic zone, but obviously in different depth layers and to a different extent.

The narrowest range was observed in *S. ahlstromi*. The 17 specimens taken recently

were found between 36 and 41°S only; the largest specimen measured 79,5 mm SL only, and all were taken at depths shallower than 200 meters.

Adolescents of *S. meadi* (11 specimens) were taken also in the northernmost stations of our transects, between 35 and 43°S, but a single halfgrown specimen of 205 mm was taken at 47°45'S in 210 m depth.

The most common species, *Luciosudis normani* (44 specimens), occurred southward again to about 47°S. Larger juveniles and semiadult specimens prevailed, and the depth range was

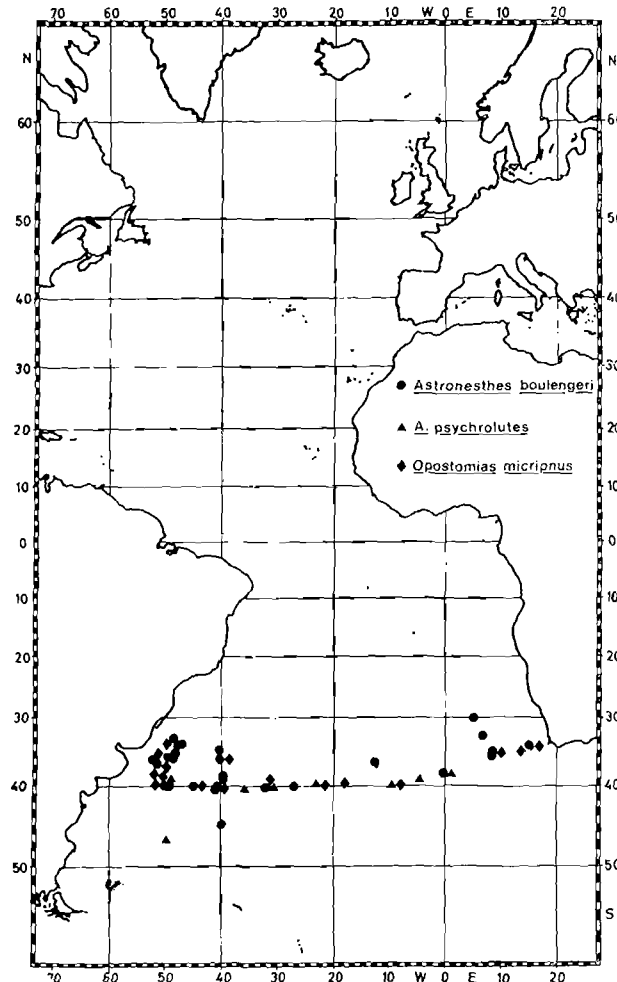


FIGURE 3

about 200 to 800 meters. Adults were taken by us during a previous cruise (1968) in spawning condition inside the Subtropical Convergence area; their larvae emigrate into the subtropical belt to return after metamorphosis as small adolescents to the Convergence area.

The southernmost species of the family is *Scopelosaurus hamiltoni*. Whereas the just metamorphosed adolescents school during the night at depths somewhat deeper than 100 meters, the few larger juveniles and adults known as yet seem to prefer depths below about 500 meters. During the 1971 cruise we took 7 small adolescents measuring 49,8 to 65,8 mm between latitudes 34°25' and 40°18'S. The smallest specimen of the Antarctic Expedition 1975/76 measured 78 mm; it was taken at 43°31'S. A second juvenile of 107 mm SL was found at 46°27'S, a halfgrown specimen of 203 mm at 54°07'S, and a still larger one of 275 mm at 59°51'S.

54°54'W, beyond the Antarctic Convergence, representing the southernmost capture of a notosudid fish as far known. Since all identified larvae of *Scopelosaurus hamiltoni* have been taken inside or just to the north of the Subtropical Convergence (BERTELSEN, KREFFT and MARSHALL, 1976), spawning of this species probably is restricted to Convergence waters; juveniles and adults migrate southward like other notosudids, but cover far greater distances, probably due to their greater strength and/or longer life span. The species grows up to at least 450 mm SL and is the largest representant of the family.

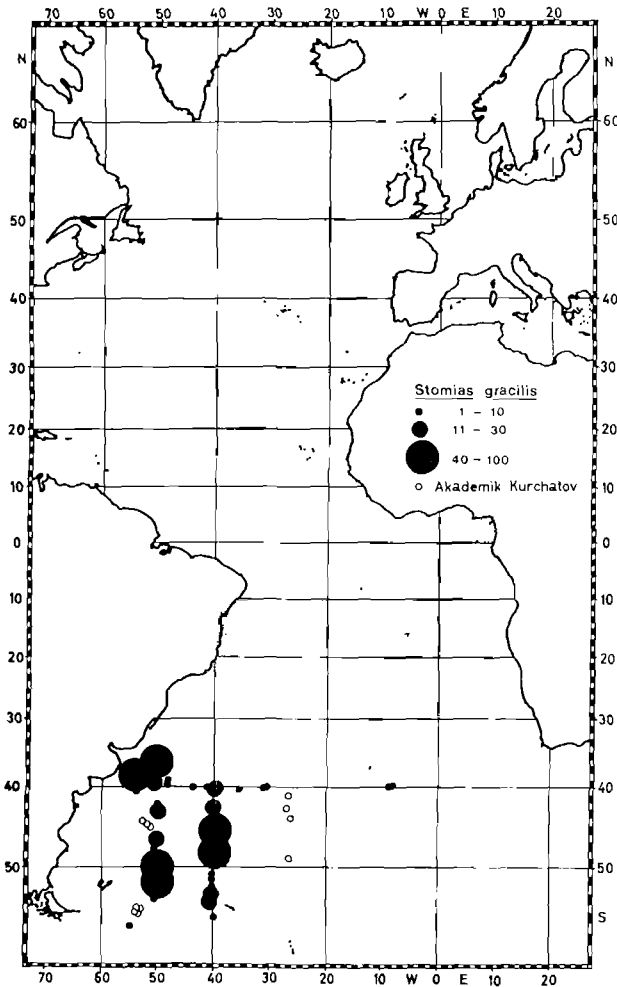


FIGURE 4

Typical examples for the Convergence Pattern are shown in fig. 3. The map is based on 56 specimens of *Astronesthes boulengeti*, 10 *A. psychrolutes*, and 29 *Opostomias micripnus*.

Figure 4 exemplifies the Subantarctic Pattern. Here, one mesopelagic species, *Stomias gracilis*, is shown. The distribution of 502 specimens taken by the «Walther Herwig» and 25 recorded by PARIN *et al.* (1974) from the «Akademik Kurchatov» is drawn. During the night hours *Stomias gracilis* may occur exceptionally as shallow as 100 to 200 meters, but in very small numbers (2% of the total catch). During daytime most were taken deeper than 900 to 1 000 meters (36,4%), the preferred night depth was 600 to 800 meters (47%). According to GIBBS (1969) «this species remains throughout its vertical migration almost entirely in intermediate water of Antarctic origin». This fact probably explains the effectiveness of the Subtropical

Convergence as a barrier for vertically migrating species, which are closely adapted to a single water mass. However, such an explanation does not hold for bathypelagic species, which do not perform vertical migrations during the dark hours. These species still can be confined in the subantarctic zone, although they could range within the Antarctic Intermediate Water far northward. Probably, there are biological parameters responsible for preventing such species from emigrating from their habitat. Such parameters could be a decrease of food below the much less productive central waters, or competition between ecologically similar species. In contrast to *Stomias gracilis*, which is replaced to the north in the Subtropical Convergence by its congener

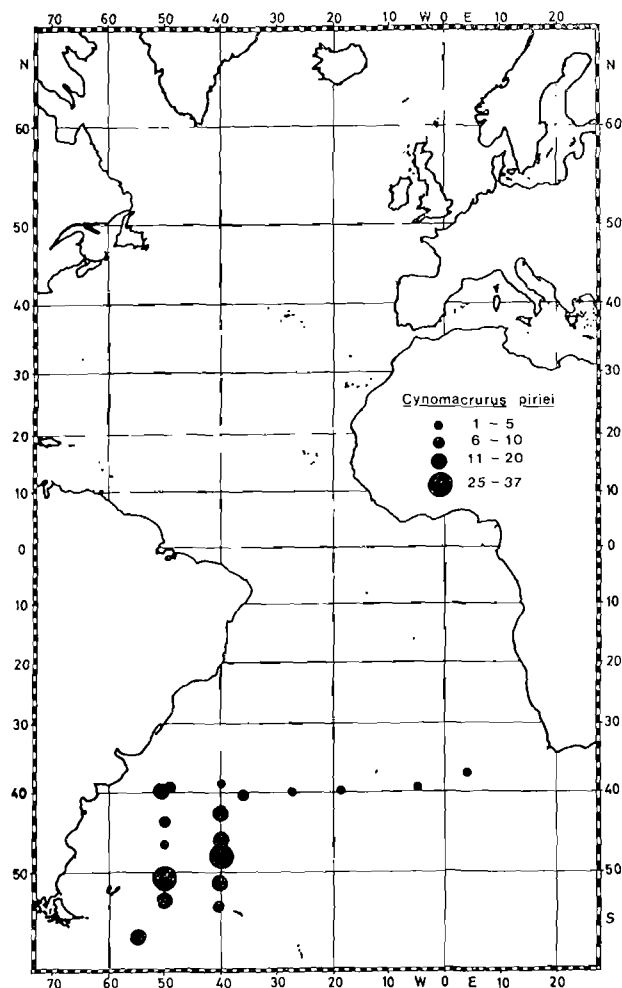


FIGURE 5

Stomias boa boa, competition seems to be excluded from the limiting parameters in cases like that of the macrourid fish *Cynomacrus piriei* (fig. 5). This bathypelagic species exhibits almost exactly the same distribution pattern as *S. gracilis* does. The «Walther Herwig» captured 201 specimens. Of these 30 (15%) were taken in hauls fishing between 700 and 1 000 meters, whereas 171 (85%) came from hauls fishing in 1 850 to 2 350 meters.

Of the 115 non-myctophid species collected by us on the two transects of the first leg of the Antarctic Expedition not more than 15 species can be allotted to a definite Subantarctic Pattern. These are listed in table 1. The remaining 100 species are composed of representatives of a wide variety of distribution patterns. The greatest number seems to be widespread, if not

cosmopolitan; these are bathypelagic species mainly. Moreover, Southtemperate, Bitemperate, Subtropical, and even broadly Tropical Patterns are involved. The *Myctophidae*, a family contributing very characteristically to the Subantarctic Pattern, is excluded in order not to anticipate results of HULLEY's coming paper.

| Family | Genus and Species | Allocated by PARIN <i>et al.</i> |
|-----------------------|---------------------------------|-------------------------------------|
| <i>Argentinidae</i> | <i>Nansenia sp.</i> | Subantarctic |
| <i>Bathylagidae</i> | <i>Bathylagus sp. I</i> | — |
| | <i>Bathylagus sp. II</i> | — |
| <i>Photichthyidae</i> | <i>Woodsia meyerwaardeni</i> | — |
| <i>Stomiidae</i> | <i>Stomias gracilis</i> | Subantarctic |
| <i>Scopelarchidae</i> | <i>Benthalbella elongata</i> | Antarctic |
| | <i>Benthalbella macropinna</i> | Subantarctic |
| <i>Paralepididae</i> | <i>Notolepis coatsi</i> | Antarctic |
| | <i>Notolepis s.n.</i> | — |
| <i>Macrouridae</i> | <i>Cynomacrurus piriei</i> | Subantarctic |
| <i>Melanonidae</i> | <i>Melanonus gracilis</i> | Subantarctic |
| <i>Melamphaeidae</i> | <i>Sio nordenskjoldi</i> | Peripheral |
| <i>Gempylidae</i> | <i>Paradiplospinus gracilis</i> | Subantarctic |
| <i>Centrolophidae</i> | <i>Icichthys australis</i> | Subantarctic |
| <i>Ceratidae</i> | <i>Ceratias tentaculatus</i> | — |

TABLE 1. — Preliminary List of Species Assigned to the Subantarctic Pattern.

Summarizing then, the Subantarctic or Notalian Zone as proposed by PARIN *et al.* (1974) is inhabited by a speciose ichthyofauna of widely different origin. The high number of endemic species corroborates the independence of the zone. However, it is felt, that the Notalian Zone lodges a fairly complex fauna contributing to a number of distribution patterns. Moreover, it ought to be differentiated into a northern sector inhabited by a mixed fauna of temperate, subtropical, broadly tropical and « Southern Subtropical Convergence » species, and a southern sector, roughly between 45° S and the Antarctic Convergence, inhabited by strictly subantarctic, bitemperate and many widespread species as well as by those which may be called « antarctic » for the time being. In the absence of any proof that there are any typical oceanic midwater fish species, the reproductive area of which is entirely confined to the waters south of the Antarctic Convergence, we still prefer to call those species spawning in subantarctic as well as in antarctic waters « Broadly Antarctic ». Many more investigations, especially in the Indian and Pacific sectors of the Southern Ocean are needed before we can understand definitively the various distribution patterns of the fauna inhabiting this ocean.

3) Types of distribution in some deep-mesopelagic and bathypelagic fish.

Systems of ichthyogeographical regions and provinces designed so far for oceanic midwater species are based usually on the common small-sized, « planktonic » species easily obtained by the Isaacs-Kidd Midwater Trawls. Most of these fishes execute diurnal vertical migrations. Very much less is known, however, about the distribution patterns of relatively deep-living mesopelagic species, which do not migrate to the surface layers, and still less about those of bathypelagic fishes. The discrepancies in the coverage of these groups are caused partly by the fact, that the smaller gear is not very well suited to collect these « rare » fishes in numbers, partly by unsolved taxonomic problems in several groups.

Therefore, it may be interesting to investigate, whether such fishes are distributed in much the same ways as the small migratory species or whether they must be assigned to different patterns. No unequivocal answer can be given to that question, but certain trends may be shown by the following examples.

Let us consider first a few midwater species which most probably belong to the group of «vertical non-migrators». Figure 6 shows the distribution of *Opisthoproctus grimaldii* according to our captures. Of the 55 specimens, 34 (61,8 %) were obtained at depths ranging from 300 to 400 meters, 7 (12,7 %) from 400 to 700 meters. The remaining 14 specimens were probably contaminants, being taken in deep hauls fishing between 800 to more than 2 000 meters.

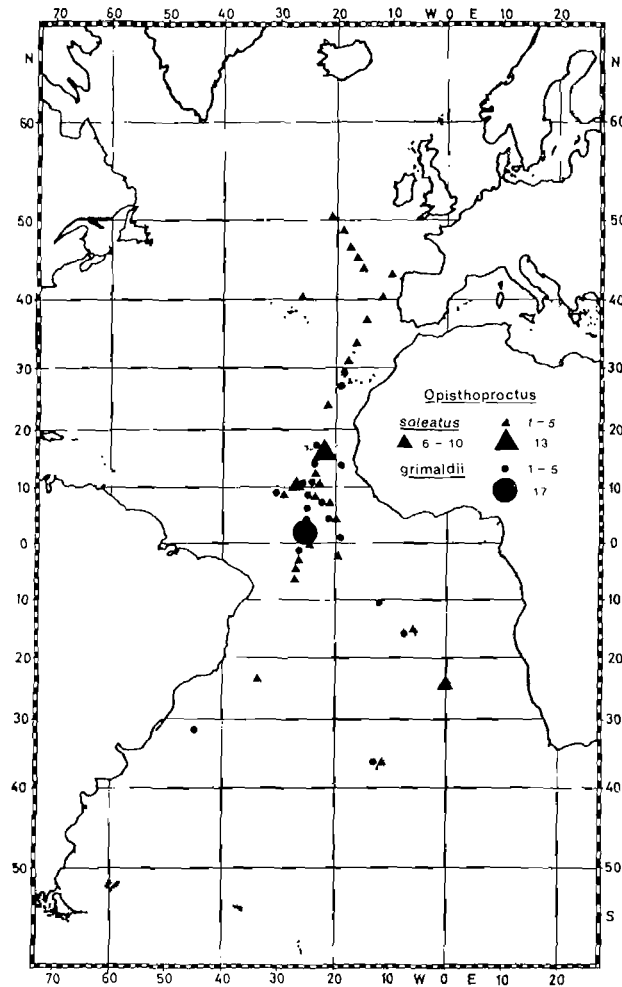


FIGURE 6

O. grimaldii is largely confined to a single water mass, the South Atlantic Central Water, and mainly concentrated in the tropical North Atlantic. A few specimens were found in the area of the South Atlantic Subtropical Convergence, and two in the vicinity of the Canary Islands. However, a few records exist in the literature of specimens taken as far north as the Azores and the Gulf of Cadiz, i.e. just beyond the northern boundary of the North Atlantic Subtropical Region. In the western North Atlantic *O. grimaldii* is known from a few catches in subtropical

waters; BEKKER (1968) found it also in the western tropical Pacific. The limits of its distribution are marked by the 10° C-isotherm and the 34,8‰-isohaline.

Its only congener, *Opisthoproctus soleatus*, is shown on the same map. In the Atlantic Ocean we found a very close correspondence between both *Opisthoproctus* species in the center of distribution and in the South Atlantic, but the range of *O. soleatus* extends to about 50° N in the eastern North Atlantic. Although taken occasionally in the same hauls, *O. soleatus* is the deeper-living species. Its center of depth distribution is between 500 and 700 meters, where 41

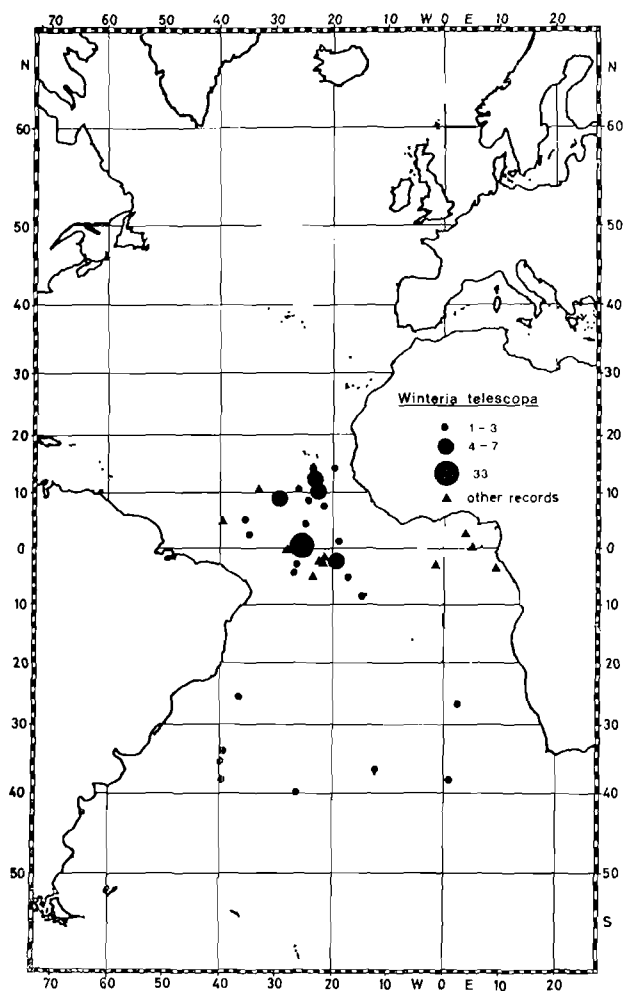


FIGURE 7

(58.6% of the 70 specimens were taken. Two specimens only were caught at depths between 300 and 400 meters, and 10 (14.3%) between 700 and 800 meters. BEKKER (1968) distinguished four separate parts of the distribution area of the species. based on literature and catches of the Soviet research vessels. According to him the Atlantic range of the species would be 1) « the central waters of the North Atlantic between 20 and 40° N with a region of emigration in the northeastern part of the ocean, in the zone of the North Atlantic Current » ; 2) the « equatorial waters of the eastern Atlantic (Gulf of Guinea and southward approximately to 10-12° S) ».

The other two distribution areas concern the Indian and Pacific Oceans. As shown in fig. 6, there is no gap in the Atlantic distribution area that would suggest the existence of two disjunct

ranges. The northern and southern boundaries of the species coincide with the 400 m-isotherm for 8° C as drawn by SCHOTT (1944). Both Central Water Masses are inhabited, but the areas of the great gyres in both hemispheres seem to be avoided by both *Opisthoproctus* species, most probably due to the very low productivity of these waters. Although still a « Tropical Pattern », that of *O. soleatus* shows a slight tendency to a northward shift.

HAEDRICH and CRADDOCK (1968) discussed the circumglobal distribution of another opisthoproctid fish, *Winteria telescopa*, based on the 23 specimens known at that time. According to them

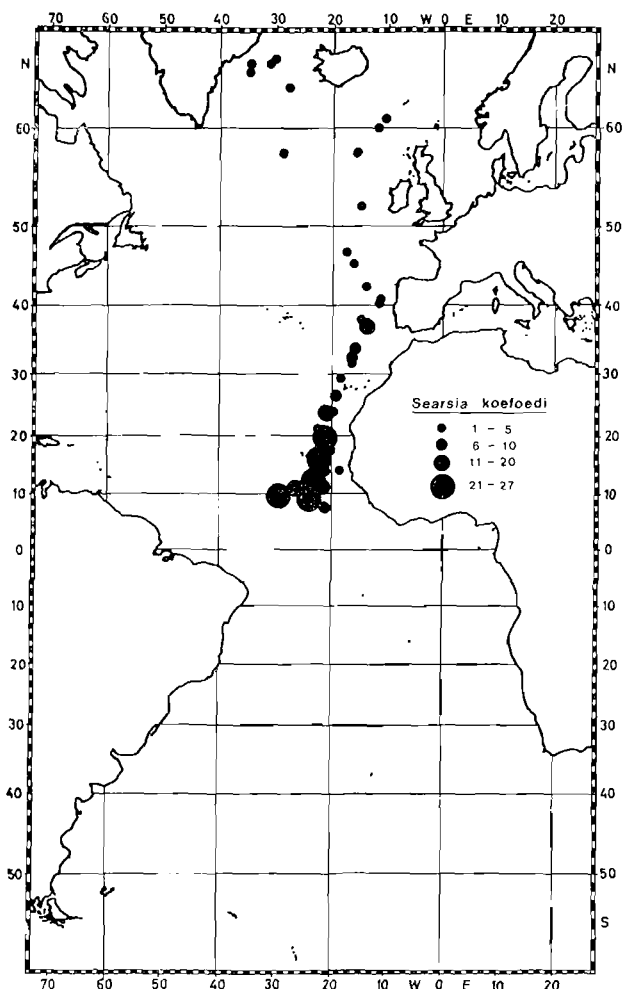


FIGURE 8

the shallowest possible depth-of-capture would be « certainly greater than 200 meters » and the main depth range 500 to 700 meters, thus equalling that of *O. soleatus*. They found, that the species occurs, « for the most part, in the transitional regions between water masses, areas where the productivity is probably higher than in the generally poorer waters of the central gyres ». Moreover, HAEDRICH and CRADDOCK suggest that the distribution of *Winteria* may be determined at least in part by water density. Figure 7 presents the distribution data of 89 specimens caught by German research vessels and 11 taken from the literature, amounting to a total of 100 specimens. The new figures limit the shallowest probable depth of capture to about 430 meters

and corroborate the expected main depth range of 500 to 700 meters, where 65 (73 %) of the 89 specimens were taken. In addition 23 specimens were captured in nets fishing at depths ranging from 1 300 to 2 400 meters; these are considered as being contaminants. This is a deep-mesopelagic fish representing definitely the tropical distribution pattern. Its northern boundary corresponds to that between South Atlantic and North Atlantic Central Water whereas the southern boundary is marked by the South Atlantic Subtropical Convergence. The specimens

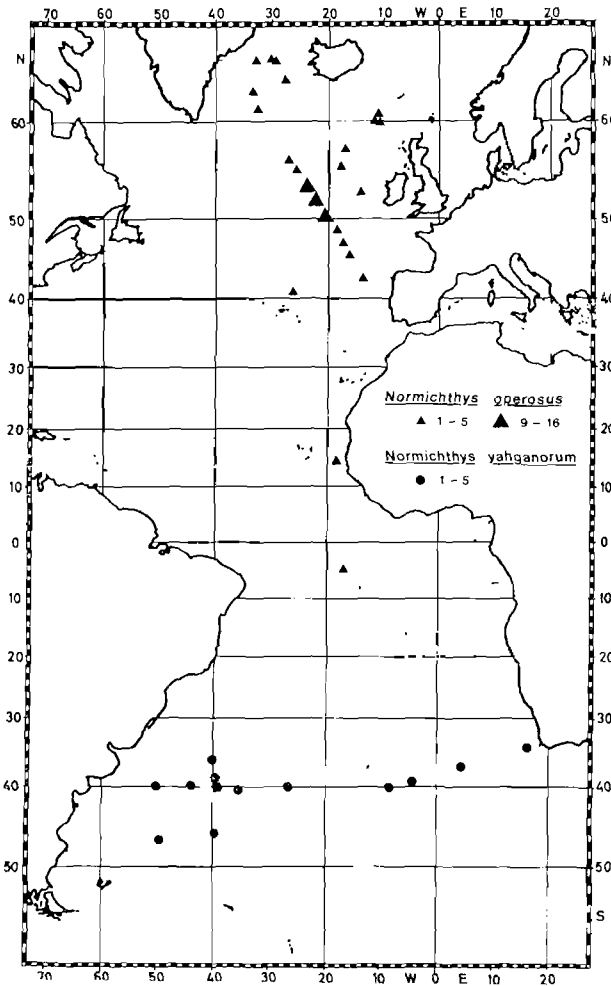


FIGURE 9

caught in the subtropical South Atlantic are most probably waifs drifting out of the species' reproductive area in the South Equatorial and the Brazil Currents. *Winteria* is living mainly at the bottom of the South Atlantic Central Water, i.e. the layer bordered below by the underlying Antarctic Intermediate Water as shown by LENZ (1975). The density isopleths superimposed on the T-S diagram of LENZ do not contradict HAEDRICH and CRADDOCK's suggestion of a depth distribution depending in part on density, but the restriction in range by density as a limiting factor seems difficult to demonstrate. PARIN *et al.* (1974) assign to *Winteria* an equatorial distribution pattern, adding that the species inhabits subtropical waters in the Pacific and Indian Oceans.

A North Atlantic Subtropical Distribution Pattern, though not as well-defined as in some myctophids and gonostomatids is shown by the searsid fish *Searsia koefoedi* (fig. 8). Like

many subtropical organisms, this species ranges far northward in the eastern half of the Atlantic Ocean, where warm and highly saline water is carried by the North Atlantic Current or one of its branches, the Irminger Current, almost to the border of the Subarctic Region. The map is based on 265 specimens of *S. koefoedi*, 255 of which were taken by the pelagic trawls, and 10 by bottom trawls. The shallowest depth-of-capture observed was 400 to 500 meters, where two specimens (0,8 %) of the pelagic catches were taken. The main concentrations were in 500 to 600 meters depth (62,7 %); another 0,8 % was taken in 600 to 700 meters. However, these shallower concentrations were only observed near the northern and southern boundaries of the species' range; in the centre of this range, where the warm and more saline water goes much deeper, the species was taken mainly in deep hauls fishing deeper than 1 000 meters. The same observation could be made from bottom trawl captures.

The horizontal range of *S. koefoedi* seems to be limited by the 400 m-isohaline for 35 ‰ as drawn by DEFANT (1961 : pl. 6). The southern boundary is sharply marked by the line to which the Antarctic Intermediate Water penetrates to the northward in 500 meters depth, coinciding with the area of the Equatorial Counter Current. The northern boundary - and the eastern too - are formed by the secondary Polar Fronts. Outside the eastern North Atlantic the species is known from the subtropical western North Atlantic and from the Indo-Australian region.

Two other searsid species, *Maulisia maui* and *Sagamichthys schnakenbecki*, show almost exactly the same pattern.

Generally, searsid fishes exhibit well-defined distribution patterns. This has been shown previously for two of the shallower-living species, *Paraholtbyrnia cyanocephala* and *Persparsia kopua* (KREFFT, 1974). The Subarctic - North Temperate Pattern can be exemplified by *Normichthys operosus* (fig. 9), a species living at the bordering layer between the mesopelagic and the bathypelagic realms at about 1 000 meters depth. Of the 91 specimens caught by our research vessels only four were found south of the North Atlantic Temperate region, three of them in the upwelling zone off Dakar where several characteristic inhabitants of the Subarctic - North Temperate fauna are encountered, and a single probably expatriated specimen far outside of the normal range of the species. The northern and western boundaries of the distribution area seem to follow the 1 000 m-isotherm for 4° C, the Southern boundary that for 5°.

The second Atlantic species, *Normichthys yahganorum*, represents the Subtropical Convergence Pattern as shown on the same map (fig. 9). The « Walther Herwig » captured 24 specimens, all of them taken exclusively in hauls fishing at depths ranging from 785 to more than 2 000 meters, most probably at the bottom of the Antarctic Intermediate Water. The Convergence Pattern has been discussed already.

With increasing depth of species occurrence the boundaries between neighbouring faunal provinces and regions show a tendency to become weak, but can be still observed in a number of species. Unfortunately, many gaps still exist in our knowledge of the bathypelagic distribution patterns, especially in the western North Atlantic. This is true, e.g., for a number of alepocephaloid species, which seem to be restricted in their distribution to the eastern part of the ocean. Since some of them are apparently adapted to specialized habitats, their absence in the western South Atlantic could possibly be explained by the fact that the deep hauls of our ships in the area concerned did not include such habitats. As examples the distribution patterns of the alepocephalid fish *Photostylus pycnopterus* (fig. 10) and of the two searsid fishes of the genus *Barbantus* (fig. 11) are given. In 1969 GOODYEAR reported on new records of *Photostylus* in the Indian and Pacific Oceans. He found the species to be associated with « steeply inclined topography : either continental or island margin, or oceanic ridge ». At least 26 specimens have been found since, including 10 from German research vessels. The Atlantic records are shown in fig. 10, except for two « Oregon » specimens taken in the Gulf of Mexico. They show, that *Photostylus* is widely spread over the North Atlantic from the East Greenland slope to the islands in the Gulf of Guinea, and from here to the Gulf of Mexico. Its depth distribution ranges from 645 to 740 meters in the Gulf of Guinea to perhaps more than 2 000 meters in the Gulf of Mexico and the western Atlantic, suggesting a remarkable independence from water masses. The association with steeply inclined topography, however, is

corroborated by all available records. In the South Atlantic the species still has not been found. Actually, we did a number of deep hauls around St. Helena and Ascension Islands in 1967 and repeated them in 1971, all of them negative as far as *Photostylus* is concerned.

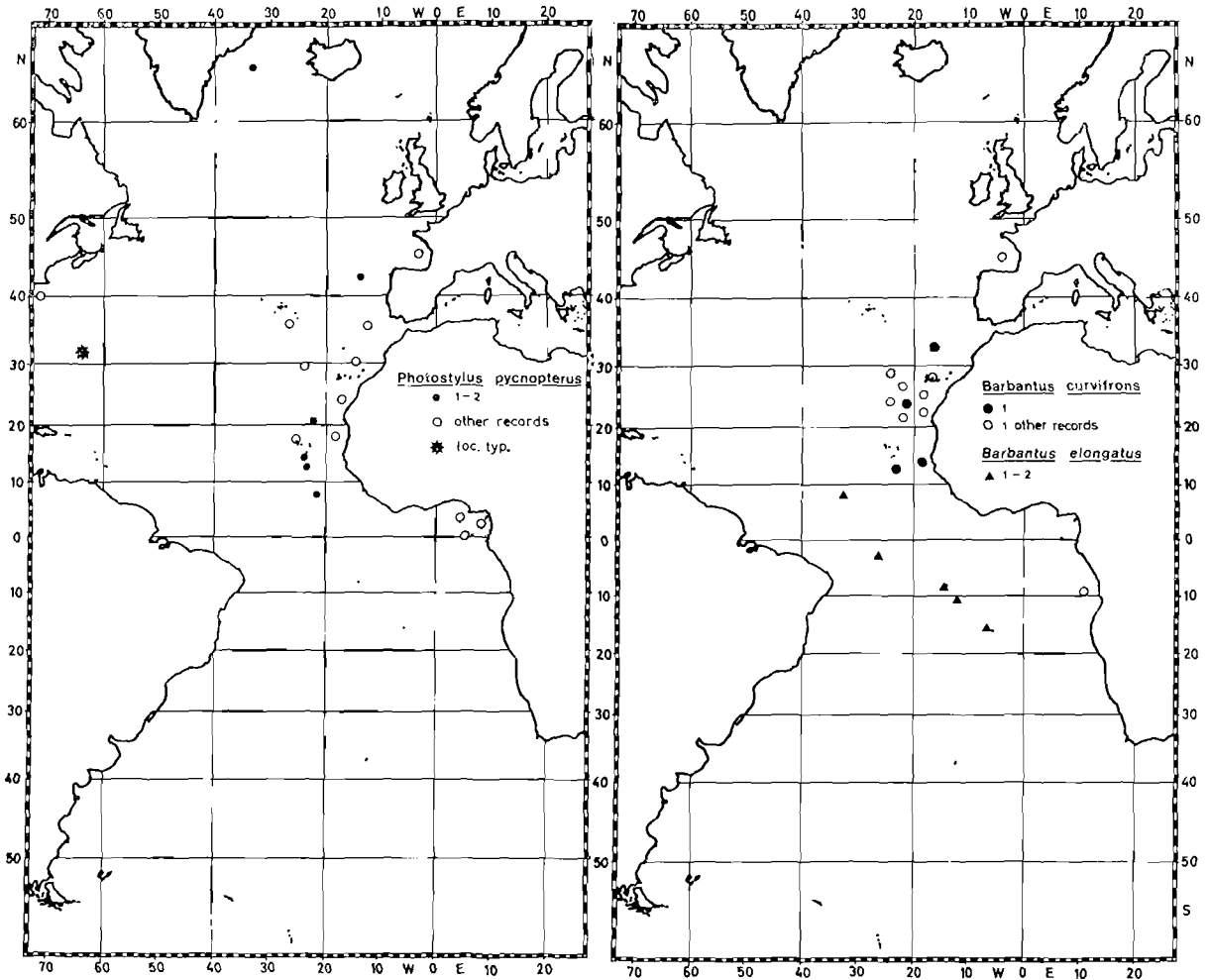


FIGURE 10

FIGURE 11

The distribution patterns of *Barbantus curvifrons* and *B. elongatus* (fig. 11) suggest a similar association. *Barbantus curvifrons* is known from only 15 specimens, two of them taken in the Indian Ocean. Except for one specimen taken by the « Ombango » off Angola, the remaining 12 Atlantic specimens came from the eastern North Atlantic, mainly from off Madeira, the Canary Islands and the Cape Verde Islands. None has been recorded from the western Atlantic as yet. The shallowest record again is that from the Gulf of Guinea, 800 meters, the remaining specimens were captured at depths exceeding 1 000 meters.

The second species of *Barbantus*, *B. elongatus*, appears to be closely associated with the slopes of St. Helena, Ascension, and with the Mid-Atlantic Ridge. This species is known from only seven specimens, captured at five stations. The depth range observed was from 1 800 to 2 000 meters. The 1 000 m-isotherm for 5° C, and the respective isohaline for 34.75‰ keep the two species apart according to the few data at hand.

The eastern slope of the Mid-Atlantic Ridge may be considered for the time being as the western boundary of the distribution area of several alepocephaloid species never taken in our many deep hauls to the west of the ridge. Examples are: the searsid fish *Pellisolus*

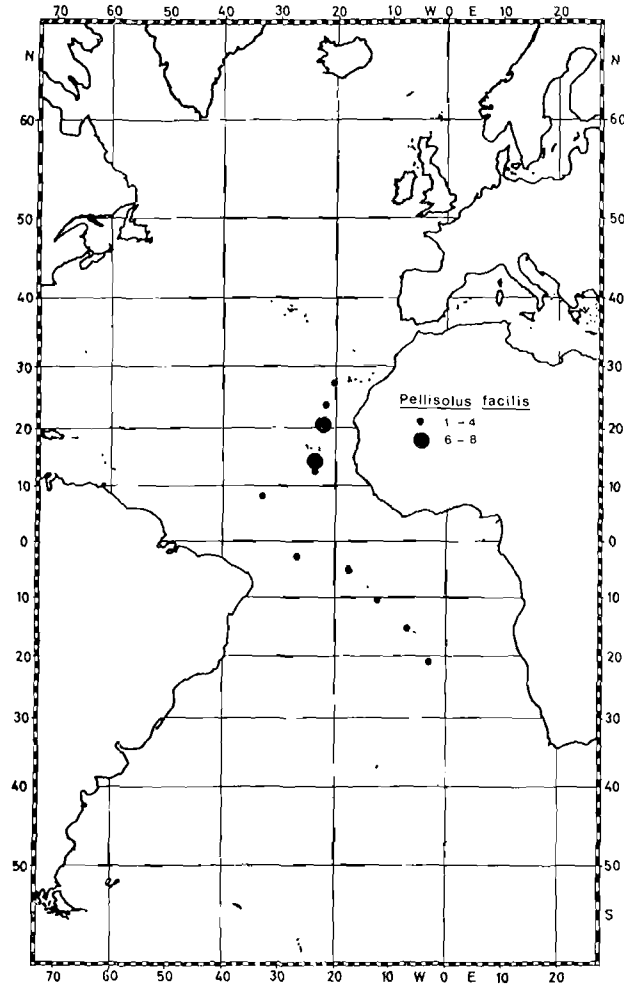


FIGURE 12

facilis, represented in our Atlantic collections by 32 specimens (fig. 12), and a number of rare alepocephalids, e.g. *Einara macrolepis*, *Asquamiceps* sp. n., and *Bathytroctes oligolepsis*, the latter listed previously as *Grimatroctes*. All of these are closely associated with the Mid-Atlantic Ridge; none is known from the western side.

All of these species are sluggish, obviously slow-swimming plankton feeders, soft-bodied and with a more or less feebly developed muscular system. Their restricted distribution may perhaps result from an inability to compete with more active and agile species; therefore they are confined to peculiar habitats.

On the screen of powerful echo sounders concentrations of scatterers often can be seen on the «windward side» of submarine ridges and seamounts and on steeply inclined slope areas. Such concentrations may be swept together or attracted and maintained by deep currents, upwelling and other physical phenomena or by associated biological productivity. We know that many of the sluggish benthopelagic species, especially alepocephalids, prefer corresponding

localities on the continental slopes where they represent a prominent part of the fish communities. Seamounts and submarine ridges apparently play the same rôle for bathypelagic members of the same or closely related families in the open ocean.

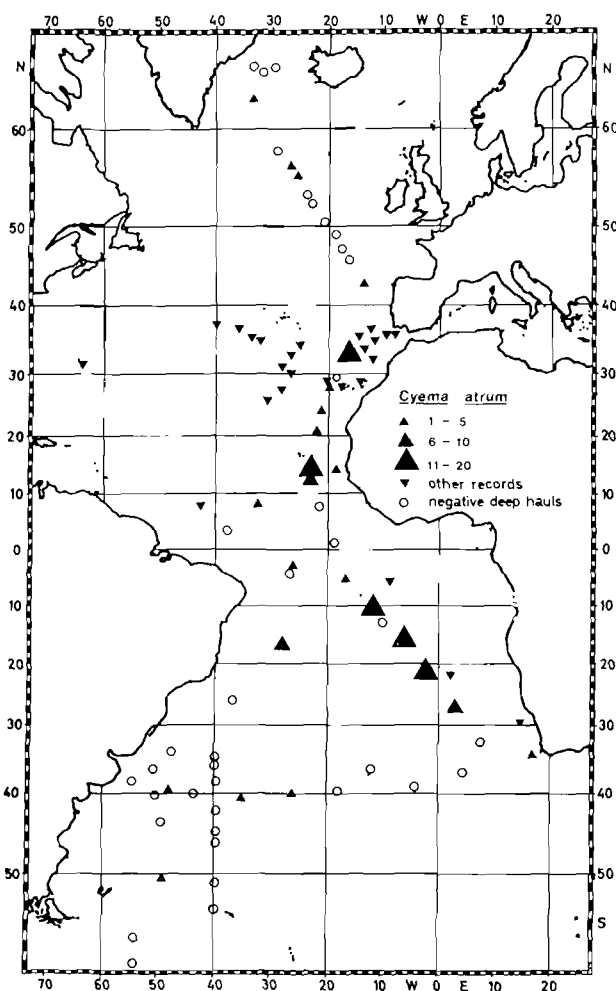


FIGURE 13

Quite distinct from such topographically bounded distribution patterns are those of the majority of bathypelagic fishes. Most of these, predatory species as well as plankton feeders, are widespread due to the greater uniformity of environmental conditions in the depths below the equatorial and central water masses. The Bobtailed Snipe Eel (fig. 13) shows this pattern quite well. Similar patterns could be shown for quite a number of species. Some of the deeper living mesopelagic species like *Malacosteus niger*, *Anoplogaster cornuta* and many others exhibit the same patterns. They are absent only in areas of a very low productivity. This has been shown earlier for bathypelagic fishes by myself (KREFFT, 1974, *Bathylaconidae*) and by JOHNSON and COHEN (1972) for the chiasmodontid genera *Dysalotus* and *Kali*.

The distribution patterns of bathypelagic fishes seem often to be governed by parameters other than those responsible for the distribution of mesopelagic fishes. We are still only

beginning to lift the veil covering the great depths. Much effort will be needed to proceed further, and close collaboration of biologists and physical oceanographers will be required. Exploration of deep circulation in the oceans is advancing rapidly in recent years. This kind of progress should result also in an improved understanding of the principles essential for understanding the geographic distribution of the bathypelagic fauna.

REFERENCES

- BACKUS (R.H.), CRADDOCK (J.E.), HAEDRICH (R.L.) and SHORES (D.L.), 1970. — The distribution of mesopelagic fishes in the equatorial and western North Atlantic Ocean. — *J. mar. Res.*, **28** (2) : 179-201.
- BACKUS (R.H.) and CRADDOCK (J.E.). — Pelagic faunal provinces and sound-scattering levels in the Atlantic Ocean. In: *Oceanic sound-scattering prediction*. — ANDERSEN (N.R.) and ZAHURANEC (B.J.), ed. — *Marine Science*, **3**, Plenum Press (in press).
- BACKUS (R.H.), CRADDOCK (J.E.), HAEDRICH (R.L.) and ROBINSON (B.A.). — A contribution to the zoogeography of the pelagic Atlantic Ocean (in preparation).
- BADCOCK (J.) and MERRETT (N.R.), 1976. — Midwater fishes in the eastern North Atlantic — I. Vertical distribution and associated biology in 30° N, 23° W, with developmental notes on certain myctophids. — *Progr. Oceanogr.*, **7** : 3-58.
- BEKKER (V.F.), 1968. — New data on mesopelagic fishes of the genus *Opisthoproctus* VAILLANT. — *Probl. Ichthyol.*, **8** (2) : 189-193.
- BEKLEMISHEV (K.V.) and PARIN (N.V.), 1960. — Biogeographical boundaries in the pelagic zone of the North Pacific in the winter of 1958-1959. — *Trudy Inst. Okeanol. AN SSSR*, **41** (in Russian).
- BERTHLEN (E.), KREFFT (G.) and MARSHALL (N.B.), 1976. — The fishes of the family *Notosudidae*. — *Dana Rep.* n° 86.
- BOGOROV (V.G.), 1959. — The biological structure of the ocean. — *Dokl. AN SSSR*, **128** (4) (in Russian).
- DEFANT (A.), 1961. *Physical Oceanography I*, 729 p., PERGAMON Press.
- DIETRICH (G.), 1964. — Oceanic Polar Front survey in the North Atlantic. — *Res. Geophys.*, **2** : 291-308.
- GIBBS (R.H. jr.), 1969. — Taxonomy, sexual dimorphism, vertical distribution and evolutionary zoogeography of the bathypelagic fish genus *Stomias* (Stomiidae). — *Smithsonian Contr. Sci.*, n° 31.
- GOODYEAR (R.H.), 1969. — Records of the alepocephalid fish *Photostylus pycnopterus* in the Indian and Pacific Oceans. — *Copeia* (2) : 398-400.
- HAEDRICH (R.L.) and CRADDOCK (J.E.), 1968. — Distribution and biology of the opisthoproctid fish *Winteria telescopa* BRALLER 1901. — *Breviora*, n° 294 : 1-11.
- JOHNSON (R.K.), 1974. — A revision of the alepisauroid family *Scopelarchidae* (Pisces: Myctophiformes). — *Fieldiana, Zool.*, **66**, V : 249 p.
- JOHNSON (R.K.) and COHEN (D.M.), 1972. — Results of the research cruises of FRV « Walther Herwig » to South America. XXX. Revision of the chiasmodontid fish genera *Dysalotus* and *Kali*, with descriptions of two new species. — *Arch. FischWiss.*, **25** (1-2) : 13-46.
- JÓNSSON (G.), 1968. — Sitthvad um sjaldgæfa fiska. — *Náttúrufr.*, **37** (1967) : 193-205.
- 1970. — Die isländischen Seefische. — *Rit Fiski deildar*, **4** (7) : 1-27 (in Icelandic and German).
- 1973. — Sjaldsédur fiskar árid 1972. — *Aegis*, 1973, 7 p.
- 1974. — Sjaldsédur fiskar árid 1973. — *Aegis*, 1974, 2 p.
- 1975. — Skrá um íslenska fiska ásamt lýsingu á nokkrum þeirra. — *Hafrannsóknir* (7) : 1-76.
- KREFFT (G.), 1974. — Investigations on midwater fish in the Atlantic Ocean. — *Ber. dt. wiss. Komm Meeresforsch.*, **23** (3) : 226-254.
- LENZ (W.), 1975. — Untersuchungen zur inneren hydrographischen Struktur des südlichen und mittleren Atlantiks (0-2000 m Tief) mit zoogeographischen Anmerkungen. — *Ber. dt. wiss. Komm Meeresforsch.*, **24** (1) : 1-22.
- MC GOWAN (J.A.), 1971. — Oceanic biogeography of the Pacific, p. 3-73. — In: FUNNELL (B.M.) and

- RIEDEL (W.R.), ed., *Micropalaeontology of oceans* Cambridge Univ.
— 1974. — The nature of oceanic ecosystems, p. 9-28. — *In*: MILLER (C.B.), ed., *The biology of the oceanic Pacific*. Oregon State Univ.
- NAFPAKTITIS (B.G.), BACKUS (R.H.), CRADDOCK (J.E.), HAEDRICH (R.L.) and KARNELLA (C.). — Family *Myctophidae*. — *In*: *Fishes of the western North Atlantic*, pt. 7. — *Mem. Sears Found. mar. Res.*, **1** (in press).
- PARIN (N.V.), 1970. — Ichthyofauna of the epipelagic zone. — *AN SSSR Inst. Okeanol.*, 1968. — Transl. Israel Program Sci. Translations. Jerusalem.
- PARIN (N.V.), ANDRIASHEV (A.P.), BORODULINA (O.D.) and TCHUVASOV (V.M.), 1974. — Midwater fishes of the southwestern Atlantic Ocean. — *In*: *Biological investigations in the Atlantic sector of the Antractic Ocean*. — *Transact. P.P. Shirshov Inst. Okeanol.*, **98**: 76-140 (in Russian).
- SCHOTT (G.). 1944. — *Geographie des Atlantischen Ozeans*. — Hamburg, BOYSEN.