Investigations on midwater fish in the Atlantic Ocean[1]

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Abstract

Investigations on board R/V "Walther Herwig" included sampling midwater fish by a large commercial midwater trawl on three meridional transects through the North and South Atlantic and one cruise from Mar del Plata to Cape Town. The observed distribution patterns of Atlantic midwater fish corroborate the findings of Backus et al. (1970) and others. In addition, they fill in a number of gaps left heretofore due to inadequate sampling, mainly in the South Atlantic. The main patterns of geographical distribution encountered along the four transects are discussed and exemplified by 14 maps.

Kurzfassung

Untersuchungen pelagischer Fische des tieferen Wassers im Atlantik. Untersuchungen der Verbreitung ozeanischer Fische des Meso- und Bathypelagials mit Hilfe von mit einem großen kommerziellen Schwimmschleppnetz vorgenommenen Fängen wurden an Bord FFS „Walther Herwig" durchgeführt. Drei Längsschnitte durch den Nord- und Südatlantik und ein Querschnitt zwischen Mar del Plata und Kapstadt liegen diesen Untersuchungen zugrunde. Die beobachteten Verbreitungsmuster bestätigen die Richtigkeit der von Backus et al. (1970) sowie von anderen Forschern erarbeiteten Befunde. Sie ergänzen diese aber auch hinsichtlich mancher Lücken, welche auf unzureichender Probenentnahme früherer Aufsammlungen, besonders im Südatlantik, beruhten. Die wichtigsten im Verlauf der vier Schnitte angetroffenen Verbreitungsmuster ozeanischer Freiwasserfische werden erörtert und an Hand von 14 Verbreitungskarten dargestellt.

The cruises and samples

From 1966 to 1971 four oceanic transects were carried out by R/V "Walther Herwig" in order to study the geographical distribution and taxonomy of the midwater fish fauna in the Atlantic Ocean. Two transects were run from the Bay of Biscay to the mouth of the La Plata River via Madeira, Canary Islands, Cape Verde Islands and Trindade Island (May 1966, January/February 1968); each of them covered about 5800 nautical miles. A third transect crossed the South Atlantic from Mar del Plata to Cape Town touching Tristan da Cunha and Gough Islands (March 1971); its length was ca. 3600 n. m. The last of these transects (April 1971) crossed the eastern Atlantic in a meridional direction from Cape Town via St. Helena, Ascension, Cape Verde and Canary Islands to Madeira and covered ca. 4800 n. m. Stations worked on all of the transects are shown in fig. 1.

Making use of the facilities of a large stern trawler we employed a large commercial 1600-meshes-herring trawl for sampling the midwater fauna instead of the more

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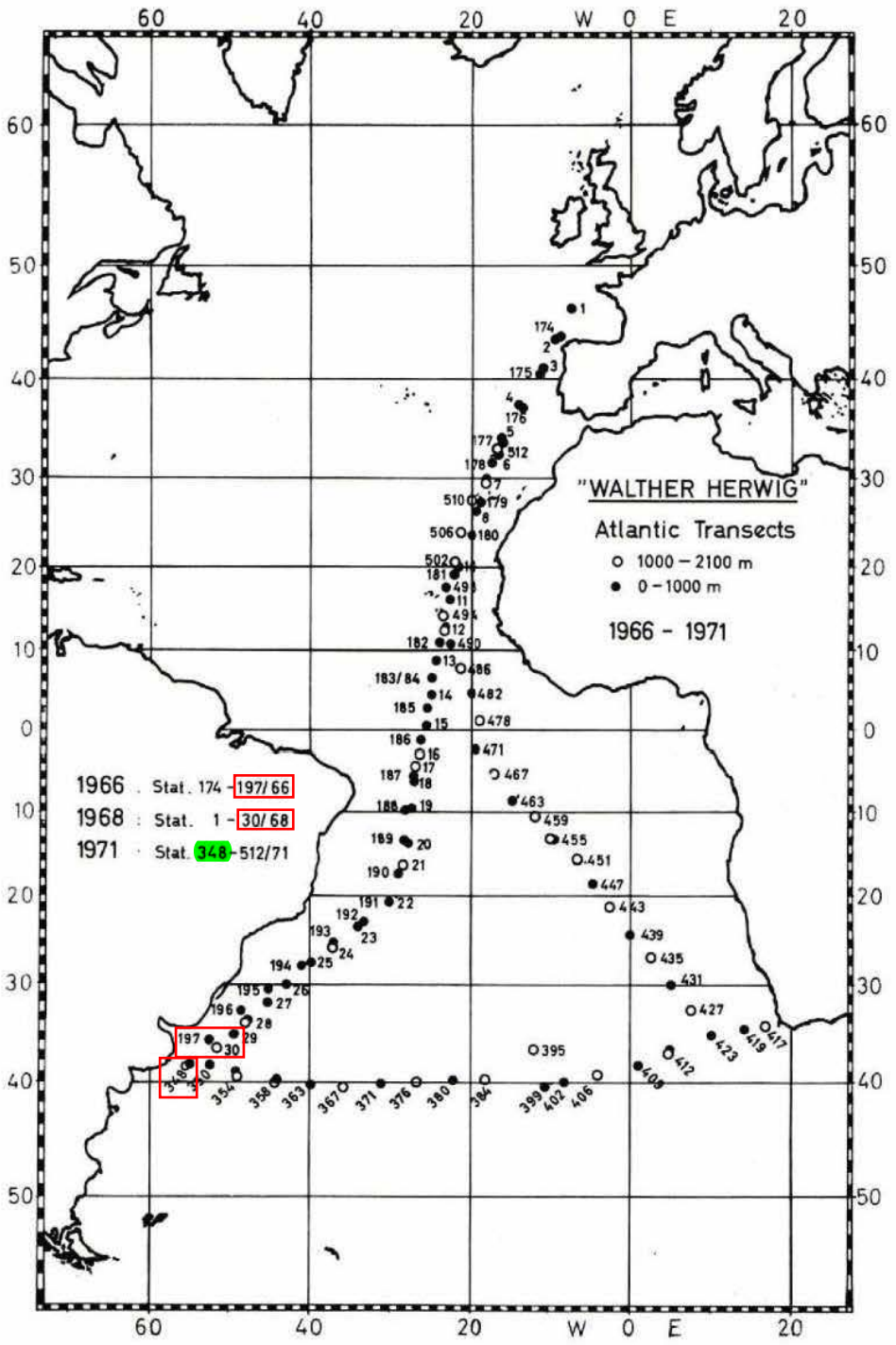

Fig. 1

conventional IKMT's or other small nets. Fishing depths were measured by using the "netzsonde" down to 1000 m, deep hauls beyond that depth were measured by using a time-depth recorder (Benthos Co.), attached to the trawl. Very few hauls were made in day-light. Most hauls were made after dusk when the fish had finished their vertical upward migrations. Step hauls at various depths, choosen according to the deep scattering layers shown on the echo sounder, were made in 1966 only. On all later cruises we towed the gear in a single layer only, starting with the shallowest selected depth, and going deeper with the next tow(s). The selected depth zones are shown in tables 1–4. Two to three hauls were executed per night, fishing starting normally at about 1900 hrs. In a few cases, shortage of time did not allow more than one haul, which was done always at a depth of ca. 2000 m. The time during which the net was towed horizontally in a selected layer ranged from 15 minutes in the shallower hauls to one hour in deep hauls at a speed of about 3½ knots. When fishing in ca. 2000 m, the process of hauling had to be interrupted twice, at depths of 1000 and 500 m for about 20 minutes each in order to cool the winch, i. e. the net started fishing horizontally again at these depths, the deep hauls actually converting into step hauls in three depth layers. Because no opening-closing device exists for large trawls, the deeper hauls may have been contaminated to some extent by specimens caught while the net was being hauled. Therefore, it is impossible to calculate actual numbers of fish/hour collected at discrete depths. Tables 1–4 give the numbers of hauls as well as those of species and specimens caught at all stations of the four transects. In addition, the geographical distribution of the stations is indicated by the vertical lines marking the latitudes of 35° N, 20° N, the equator, and 25° S in tables 1, 2 and 4. The stations are mapped, moreover, in fig. 1.

The total number of specimens taken along the four transects was 110 568. About 500 species are represented, some 40 of which are new to science. Of these, 20 have been described, most of them in the "Archiv für Fischereiwissenschaft". A number of taxonomic descriptions will also be found in revisions of families and genera published elsewhere. The number of families contributing to our catches is 89, the most important of which are the Myctophidae, represented by 24 genera, more than 90 species and 74 209 specimens.

Zoogeographical analysis

One of the major aims of our studies is the zoogeographical analysis of the species of midwater fish populating the mesopelagic and bathypelagic realms of the Atlantic Ocean. It ought to be mentioned that the terms "mesopelagic" and "bathypelagic" are used by various authors in a rather inconsistant way (e. g. Bruun 1957; Marshall 1971). Although both ecological groups of fishes differ in their respective depth distributions and also morphologically, no sharp boundaries exist between them, due mainly to the changing limits between thermosphere and psychrosphere (Bruun 1957). Marshall (1971) is followed here in calling bathypelagic those species, whose populations are centered at levels below 1000 m.

In recent years encouraging work on the distribution of mesopelagic fishes has been published (Andriashev 1962; Backus et al. 1965, 1969, 1970; Baird 1971; Bekker 1964, 1965, 1967; Bolin 1959; Bussing 1965; Ebeling 1962; Ebeling and Weed 1963; Gibbs 1969; Goodyear and Gibbs 1970; Haedrich and Craddock 1968; Mead 1972; Nafpaktitis 1968; Nafpaktitis and Nafpaktitis 1969 to mention some of the most important only). However, even in the North Atlantic we still are far from a satisfactory knowledge about the distribution patterns of mesopelagic fishes, and still farther from a thorough knowledge of the South Atlantic ichthyofauna. The

physical and biological factors controlling these patterns are complex; many of them are unknown, though a number of fruitful hypotheses have been brought forward (EBELING 1962; BACKUS et al. 1970; BAIRD 1971 among others). Analysis of our catches is still at the very beginning and will need years to be finished. Much of the material has been, and will be, distributed to specialists all over the world, and the help of many colleagues of various countries is highly acknowledged. In this paper, only a few examples of typical distribution patterns observed along our transects may be given.

Major changes in the species composition at the stations were observed at convergences, boundary areas, and in transitional areas, which formed obvious faunal boundaries. Some of these correspond closely to those shown by BACKUS et al. (1970) for the northern Atlantic.

The distribution patterns of midwater fish

The midwater fishes obtained by the "Walther Herwig" can be arranged in a number of well-defined groups on the basis of their distributional patterns. The most remarkable ones are exemplified in figs. 2–15.

I. The northern-temperate group

Several distribution patterns seem to be involved, the two most important being as follows:

a. The boreal pattern. Fish species representing the boreal pattern were found during our cruises almost exclusively north of 35° N, i. e. their southern boundary lies just north of Madeira. No seasonal differences in the distribution of such boreal species could be observed during January and May of the years investigated. The boundary coincides with the 15° isotherm at 200 m depth as drawn by BAIRD (1971). Species showing the boreal pattern are represented in our catches by a small number of samples only. Examples are *Nansenia groenlandica* (Reinhardt, 1840), *Argyropelecus olfersi* (Cuvier, 1829), *Stomias boa ferox* Reinhardt, 1843, *Myctophum punctatum* Rafinesque, 1810, *Benthosema glaciale* (Reinhardt, 1837), *Lampanyctus crocodilus* (Risso, 1810) and *Notoscopelus kroeyeri* (Malm, 1861). None of these species has a biantitropical distribution except perhaps *Argyropelecus olfersi*. This species is reported to occur in the southern Pacific between 30° S and 50° S, and in the southern Atlantic southwest of the Cape of Good Hope. However, South African specimens of "*olfersi*" I have seen obviously were not this species but misidentified *A. sladeni* Regan, 1908. According to our investigations and those of HULLEY, 1972, *A. olfersi* is absent from South Atlantic waters. Some of the other species of the boreal group range farther southward than indicated by our catches along the West African coast in the upwelling areas and in the Canary Current. As an example of the boreal pattern catches of *Myctophum punctatum* are shown along the transects run by R/V "Walther Herwig" during leg II of the "Overflow '73 Expedition" of ICES; the few positive stations of the three former cruises are included (fig. 2).

b. The temperate-subtropical pattern. Species showing this pattern have a similar distribution as those of the boreal pattern, but range farther southward finding their southern limit at about 20° N. *Ichthyococcus ovatus* Cocco, 1838, *Rhadinesthes decimus* (Zugmayer, 1911), *Hygophum benoiti* (Cocco, 1838), *Symbolophorus veranyi* (Moreau, 1888), *Diaphus holti* Tåning, 1918, *D. rafinesquei* (Cocco, 1838) and *Cera-*

toscopelus maderensis (Lowe, 1839) are examples representing this pattern. Again, none of these species is found within the southern hemisphere.

II. The subtropical group

Most of the great number of species forming this group have a biantitropical distribution in the subtropical belts of both hemispheres. Almost all of them were found between 35° and 20° N, and also between about 25° and 35° S. In the eastern Atlantic the southern subtropical belt is displaced further to the north than in the western part of the ocean, stretching to the area of St. Helena (about 16° S), and due to the cooling effect of the Benguela Current. The biantitropical subtropical pattern is exemplified by *Margrethia obtusirostra* Jespersen and Tåning, 1919, *Argyropelecus aculeatus* Valenciennes, 1849, *Astronesthes leucopogon* Regan and Trewavas, 1929, *Paralepis atlantica* Krøyer, 1868 (represented in the south by a doubtfully distinct subspecies), *Macroparalepis affinis* Ege, 1933 (fig. 3), *M. brevis* Ege, 1933 (entering the tropics by submergence from the south to about 10° S), *Hygophum hygomi* (Lütken, 1892) (fig. 3), *Diaphus effulgens* (Goode and Bean, 1896), *D. metopoclampus* (Cocco, 1829) (fig. 4), *Lampadena chavesi* Collett, 1905 (fig. 3) and *Lampanyctus pusillus* (Johnson, 1890).

Others show a similar distribution pattern, which, however, is restricted to either the northern or the southern subtropics. Such species may or may not be replaced in corresponding latitudes of the other hemisphere by closely related forms. *Idiacanthus fasciola* Peters, 1877 (North) and *I. atlanticus* Brauer, 1906 (South) are examples of such an "intrageneric bipolarity" (fig. 5). The few specimens of *I. fasciola* found in the Cape area obviously are waifs carried into the Atlantic by the Agulhas Current. One other pair to be mentioned is built by *Cubiceps gracilis* Lowe, 1843 and *C. caeruleus* Regan, 1914 (Haedrich 1972: fig. 6). Taken only in the northern subtropics were *Astronesthes neopogon* Regan and Trewavas, 1929, *Bathophilus metallicus* (Welsh, 1923), *Lampadena urophaos atlantica* Maul, 1969 and *Poromitra capito* Goode and Bean, 1883. Only in the southern subtropics the following species were found: *Neonesthes microcephalus* Norman, 1930, *Grammatostomias dentatus* Goode and Bean, 1896 (though known heretofore in the western North Atlantic only), *Myctophum phengodes* (Lütken, 1892) and *Scopelopsis multipunctatus* Brauer, 1906.

III. The tropical group

Several patterns of distribution of tropical species can be observed as exemplified by Backus et al. (1970). For our own material we distinguish the following patterns:

a. The broadly tropical pattern. This term was introduced by Backus et al. (1970) for the large group of species, whose distribution covers subtropical as well as tropical waters. During the first two transects, such species first entered our nets, as a rule, off Madeira. They then continued to be taken along the route southward to the southern Subtropical Convergence at about 35° S. Characteristic for the broadly tropical pattern are several species of myctophids, e. g. *Diaphus mollis* Tåning, 1928, *Ceratoscopelus warmingi* (Lütken, 1892) and *Notoscopelus resplendens* (Richardson, 1845). The sternoptychid fish *Argyropelecus gigas* Norman, 1930, is a further example of this pattern according to our samples; however, Baird (1971) found it "limited to transitional waters at the boundaries of tropical central or warm water masses and colder temperate waters where roughly the 5° isotherm is deeper than 800 m". The material at hand shows that dense concentrations of *A. gigas* can also be observed inside the

South Atlantic Central Water mass, where the 5° isotherm is in a depth of 650 m (stations 443 and 447/71; fig. 8).

A comparison of the distribution areas of different broadly tropical species reveals specific differences due to distinct food requirements. Thus, more pretentious species like *A. gigas* and *N. resplendens* (fig. 6) show a distinct gap in their distribution pattern off northeastern Brazil. Here, a counter-clockwise gyral is built up by the South Equatorial and Brazil Current system. The area shows great similarity to the Sargasso Sea in the North Atlantic. It is of very low productivity, as exemplified by the sharp decline in numbers of species as well as specimens in our catches at stations 189 to 190 (1966, tab. 1) and 20 to 21 (1968, tab. 2). Quite a number of common tropical and broadly tropical species are lacking here. Others, like some species of *Eustomias*, *Chauliodus danae* Regan and Trewavas, 1929 and *Lepidophanes gaussi* (Brauer, 1906), which are lacking in more productive areas and represent the "Sargasso Sea pattern" of BACKUS et al. (1970), reappear again. Since the gyral is obliquely inclined to the surface, being shallower at its northern than at its southern extremity, deeper living species like *A. gigas* show a distribution gap displaced more to the south than that of species living near the surface, such as *N. resplendens*. Smaller growing, less pretentious species like *Ceratoscopelus warmingi* (fig. 7) do not show any gaps in their distribution areas.

b. The tropical patterns. Fishes exemplifying these patterns are confined to tropical areas, i. e. the region between about 20° N and 25° S along our transects. However, the southern boundary is much less defined than the northern one. Latitudinally distributed species occurring across the tropics from west to east were found, as well as others, which were restricted either to the eastern ("Guinean pattern") or to the western ("Amazonian pattern") sections of the ocean. *Microstoma microstoma* (Risso, 1810), *Astronesthes indicus* Brauer, 1902, *Heterophotus ophistoma* Regan and Trewavas, 1929, *Stomias affinis* Günther, 1887, *Hygophum macrochir* (Günther, 1864), *Myctophum asperum* Richardson, 1844, *Lampadena luminosa* (Garman, 1899), various *Diaphus* species and many others represent the latitudinal tropical pattern. As an example the distribution of *Astronesthes richardsoni* Poey, 1853 is given (fig. 9), though its range does not cover the whole tropical belt in North-South direction.

Eastern tropical species are *inter alia Paraholtbyrnia cyanocephala* Krefft, 1967 (fig. 10), *Stomias lampropeltis* Gibbs, 1969, *Chauliodus schmidti* Ege, 1948, whereas *Diaphus garmani* Gilbert, 1906, *Brama caribbea* Mead, 1972 and perhaps also *Pseudoscopelus scutatus* Krefft, 1971 (fig. 11) represent the western pattern.

In addition, several other patterns of warm water distribution seem to be involved. Most of them exemplify either disjunct distribution areas of otherwise tropical or broadly tropical species, e. g. *Pollichthys mauli* Poll, 1953 as discussed by BACKUS et al. (1970), or rather restricted habitats, which may be explained as adaptations to land associated environments (BAIRD, 1971). Good examples of such an association are the species of the sternoptychid genus *Polyipnus*, which are represented in our material only by *P. polli* Schultz, 1961 (fig. 10). *Lampadena pontifex* Krefft, 1970 and a still undescribed *Symbolophorus* species, living in the area of the Cape Verde Islands, perhaps belong to this group of "pseudoceanic" midwater fishes.

Others, like *Argyropelecus sladeni* Regan, 1908, were found almost everywhere in the South Atlantic Central Water mass (fig. 12). However, since its main concentrations lie between 18° N and 5° S, its distribution pattern is mainly tropical.

Finally, there is one special pattern of tropical distribution, which may be called the Agulhas pattern. This is represented by a small number of tropical Indian Ocean species. Specimens of these species are carried into the South Atlantic Ocean around the Cape with the warm Agulhas Current. Their range inside the Atlantic is closely associated with the body of Agulhas Water (figs. 5 and 13). Besides *Persparsia kopua*

(Phillips, 1942), 7 specimens, *Bathophilus cwyanorum* Barnett and Gibbs, 1968, 2 specimens, *Eustomias bulbornatus* Gibbs, 1960, a single specimen, *Diaphus diadematus* Tåning, 1932, 77 specimens, *D. parri* Tåning, 1932, a single specimen, *D. richardsoni* Tåning, 1932, 4 specimens, and *Myctophum spinosum* (Steindachner, 1867), 4 specimens, the few South Atlantic specimens of *Idiacanthus fasciola* belong to this group. Except perhaps *Persparsia* and *Diaphus diadematus*, Indian Ocean expatriates do not seem to be able to survive outside the body of Indian Ocean water.

IV. The southern group

During the 1971 transect between Mar del Plata and Cape Town, which ran partly through the area of the southern Subtropical Convergence, and partly through the neighbouring waters of the Westwind Drift, R/V "Walther Herwig" met with a fish fauna quite distinct from those along the other transects. Here, a highly mixed fauna of heterogenous origin was found. Of 265 species taken in the area, 72 were not represented to the north of the convergence. These are members of the following distribution patterns:

a. The convergence pattern. Gibbs (1968) was the first author to report on a special fauna, distributed circumglobally in the waters of the southern Subtropical Convergence. Several species have been added to his list since. The following species taken by us are members of that peculiar fauna: *Astronesthes boulengeri* Gilchrist, 1902 (fig. 14), two other undescribed *Astronesthes* species, *Bathophilus ater* (Brauer, 1902), *Eustomias trewavasae* Norman, 1930, *Opostomias micripnus* (Günther, 1878) (fig. 14), *Diaphus ostenfeldi* Tåning, 1932 (fig. 4) and *Scopelarchoides kreffti* Johnson, 1972.

b. The Westwind Drift pattern. Fishes fitting this distribution pattern may be found in a more or less circumglobal belt between the Subtropical and the Antarctic Convergences, i. e. in the Antarctic Intermediate Water. A great number of species, especially myctophids, live here, e. g. the gonostomatids *Diplophos rebainsi* Krefft and Parin, 1972, *Photichthys argenteus* Hutton, 1872, *Woodsia meyerwaardeni* Krefft, 1973, the notosudids *Luciosudis normani* Fraser-Brunner, 1931 and *Scopelosaurus hamiltoni* (Waite, 1916), the myctophids *Protomyctophum subparallelum* (Tåning, 1932), *P. tenisoni* (Norman, 1930), *Electrona carlsbergi* (Tåning, 1932), *E. ventralis* (Bekker, 1963) or a closely related species, *E. subaspera* (Günther, 1864), *Hygophum hanseni* (Tåning, 1932), *Lampadena dea* Fraser-Brunner, 1949, *L. notialis* Nafpaktitis and Paxton, 1969, *Hintonia candens* Fraser-Brunner, 1949, *Gymnoscopelus bolini* Andriashev, 1962, *Lampichthys procerus* (Brauer, 1904), the melamphaeid *Sio nordenskjoeldi* (Lönnberg, 1905), the centrolophid *Icichthys australis* Haedrich, 1966, and the ceratioid *Ceratias tentaculatus* Norman, 1930.

c. The broadly Antarctic pattern. The distribution area of those species stretches from the coasts of Antarctica to the Subtropical Convergence. *Stomias gracilis* Garman, 1899, *Benthalbella elongata* (Norman, 1937), *B. macropinna* Bussing and Bussing, 1966, *Protomyctophum anderssoni* (Lönnberg, 1905), *P. bolini* Fraser-Brunner, 1949, *P. normani* (Tåning, 1932), *Electrona antarctica* (Günther, 1878), *Gymnoscopelus braueri* (Lönnberg, 1905), *G. nicholsi* (Gilbert, 1911), *Lampanyctus achirus* Andriashev, 1962, and the macrourid fish *Cynomacrurus piriei* Dollo, 1909 may be mentioned.

d. The bipolar pattern. It is represented by oYen deep-living species, which occur in subarctic as well as in subantarctic waters. Some of them, e. g. *Anotopterus pharao* Zugmayer, 1911, *Borostomias antarcticus* (Lönnberg, 1905) and *Trigonolampa miriceps* Regan and Trewavas, 1930, even penetrate subtropical areas by submergence. They are fairly common in our collections.

V. The bathypelagic group

More than 80 species, i. e. about 16 % of the total number, have been taken exclusively in hauls deeper than 800 m. As a rule, such species occupy larger geographical ranges than mesopelagic species. Their distribution areas often stretch from subarctic areas to the southern Subtropical Convergence or even beyond. *Gonostoma bathyphilum* (Vaillant, 1888), and *Malacosteus niger* Ayres, 1848 are examples. However, there are others, whose distribution, though covering enormous ranges, seems to be associated with specialized topographical conditions, e. g. steeply inclined edges of oceanic islands, submarine ridges, seamounts and continental slopes (GOODYEAR 1969). Large adults of bathypelagic species are caught more often by deep-fishing bottom trawls than by midwater trawls. This is true for many species of paralepidids, notosudids, ceratioids, gempylids and many others. Even the largest myctophids I have seen, *Gymnoscopelus (Nasolychnus)* spec. of more than 30 cm standard length, were taken by bottom trawls in 1200 m depth. From this, it appears that large adults of many bathypelagic fishes tend to become benthopelagic with age. This is well demonstrated by the alepocephalids.

Actually, the distribution of most bathypelagic species is poorly understood as yet, due to inadequate sampling. Therefore, it is difficult to assign definite distribution patterns to most of them. As an example, the distribution of the Bathylaconidae is shown here (fig. 15), based on the investigations of NIELSEN and LARSEN (1970), NIELSEN (1972) and on some additional specimens taken by R/V "Walther Herwig" during the "Overflow '73 Expedition". Two species of the family, *Bathylaco nigricans* Goode and Bean, 1896 and *Herwigia kreffli* (Nielsen and Larsen, 1970), are represented in the Atlantic Ocean. They seem to cover the same geographic range between about 54° N and 35° S, and either one or both species were taken at almost all of our stations deeper than 1000 m. They seem to be associated with the North Atlantic Deep Water mass, which is formed in the Labrador and Irminger Seas mainly, and stretches southward below the Antarctic Intermediate Water in a depth of about 1500 to 2000 m. Approximately in the area of the southern Subtropical Convergence it sinks deeper, beyond the reach of our nets. This may explain the complete absence of both species in our deep hauls along the transect Mar del Plata – Cape Town. Because of the close association with the North Atlantic Deep Water, the distribution pattern shown by the Bathylaconidae may be called the North Atlantic Deep Water pattern for the time being. The chiasmodontid fish *Kali macrodon* (Norman, 1929) seems to share the same pattern.

Other species are associated with the Antarctic Intermediate Water. The searsiid fish *Normichthys yaganorum* Lavenberg, 1965 is an example. It is replaced in the North Atlantic between Iceland and the Bay of Biscay by *Normichthys operosus* Parr, 1951.

The analysis of the bathypelagic species caught during our transects is still at the beginning. It seems obvious, that while most bathypelagic species have larger geographical ranges than mesopelagic fishes, they still show specific distribution patterns rather than a cosmopolitan distribution.

Concluding remarks

Studies on the distribution of Atlantic midwater fish reveal a highly complicated, three-dimensional cob-web of distribution patterns. Actually, each species develops its own specific pattern, depending on biotic and abiotic environmental factors as well

as on its distributional history. The demand for food, competition and different adaptability to physical conditions seem to be important. However, in spite of the diversity of specific patterns, the threads of the web join to form larger patterns, which characterize well-defined faunal communities. These populate different parts of the ocean, and are separated from each other by physical boundaries, which divide the ocean into faunistic regions. Some species inhabit a single region, others are widespread or dwell in disjunkt areas. Trenchant boundaries along our transects were found at about 20° N, i. e. the boundary between the two Central Water masses, and at the southern Subtropical Convergence. At both these boundaries a distinct change in the faunal composition could be observed. Many species disappeared from the catches in these areas and were replaced by other ones. The boundary at 20° N separates the subtropical fauna from the tropical one quite effectively; there is no distinct counterpart in the southern hemisphere, where, as a rule, both tropical as well as subtropical species find their southernmost border at the Subtropical Convergence. Also, the hypothetical boundary separating the "Guinean" from the "Amazonian" region, which should be expected somewhere along the 30th meridian W, is rather weakly defined, although a number of species obviously show either eastern or western distribution patterns.

Much work still has to be done, before we can assign a definite distribution pattern to each of our species. Such patterns seem most diverse in the group of tropical species, the most speciose fauna encountered. Life history studies, still lacking for the bulk of oceanic fishes, and careful compilation and analysis of the many distribution studies of recent and future years may one day enable us to understand the distribution patterns of deep-sea fishes.

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Summary

The paper deals with the geographical distribution of Atlantic midwater fish, based on the collections of R/V "Walther Herwig". Four transects were run during 1966 to 1971 forming a huge triangle between the Bay of Biscay, the mouth of the La Plata river and Cape Town (tabls. 1–4; fig. 1). Using a large commercial midwater trawl, more than 110 000 fish specimens, representing about 500 species and 90 families, were taken. Of these, some 40 species were new to science at the time of capture.

According to their geographical distribution, 5 groups are distinguished, each of them comprising one or several distribution patterns:

I. The northern-temperate group. A boreal (fig. 2) and a temperate-subtropical pattern are represented.

II. The subtropical group. Inside this group biantitropical patterns, either at the specific (figs. 3–4) or at the generic level (fig. 5), as well as distribution areas confined to one hemisphere only, were observed.

III. The tropical group. This is the most speciose group of fishes. The species may be assigned the broadly tropical pattern (figs. 6–8), the latitudinal tropical pattern (fig. 9), or patterns covering more restricted ranges, e.g. the Guinean pattern (fig. 10), the Amazonian pattern (fig. 11), and probably some others. Of these, the "Guinean pseudoceanic pattern" (fig. 10), the South Atlantic Central pattern (fig. 12), and the Agulhas pattern (figs. 5, 13) are presented.

IV. The southern group. This is made up by species living either in or south of the southern Subtropical Convergence area. The convergence pattern is shown (figs. 4, 14). Other species found here represent several additional patterns, viz. the Westwind Drift pattern, and the broadly Antarctic pattern.

V. The bathypelagic group. Only a few of the more than 80 species of bathypelagic fishes, inhabiting the layers of the ocean deeper than 800 or 1000 m, have as yet been analyzed with regard to their distribution. Although covering much larger ranges; when compared with those of mesopelagic fishes, bathypelagic species follow specific distribution patterns, rather than being cosmopolitan. As an example the North Atlantic Deep Water pattern is shown (fig. 15).

Zusammenfassung

Die Zoogeographie atlantischer Fische des Meso- und Bathypelagials wird in dieser Arbeit untersucht. Sie basiert auf Fängen des FFS „Walther Herwig", welche während der Südamerikareisen des Schiffes auf vier transozeanischen Schnitten in den Jahren 1966, 1968 und 1971 erzielt wurden. Die Schnitte bilden ein Dreieck zwischen dem Golf von Biscaya, der Mündung des Rio de la Plata und Kapstadt (Abb. 1). Über 110 000 Fische in etwa 500 Arten und 90 Familien wurden bei diesen Fahrten mit einem 1600-Maschen-Schwimmschleppnetz gefangen. Von ihnen waren etwa 40 Arten zur Zeit ihres Fanges noch unbeschrieben.

Das bisher aufgearbeitete Material umfaßt nur einen relativ bescheidenen Teil der Gesamtausbeute. Dennoch ergeben sich zoogeographisch interessante Verbreitungsmuster, welche die Befunde von Backus et al. (1970) vielfach bestätigen und erweitern. Auf Grund ihrer Verbreitung werden in der vorliegenden Arbeit vier Gruppen mesopelagischer Fischarten unterschieden und mit der einstweilen als Einheit behandelten Gruppe der bathypelagischen Fische verglichen. Jede der 5 Gruppen umfaßt ein oder mehrere Verbreitungsmuster.

I. Die nördlich-temperierte Gruppe. Sie ist in den Fängen der drei Expeditionen nur spärlich vertreten. Dennoch lassen sich zwei Verbreitungsmuster unterscheiden, das boreale (Abb. 2) und das gemäßigt-subtropische.

II. Die subtropische Gruppe. Dieser Gruppe angehörige Arten traten in unseren Fängen in der Regel erst bei Madeira in Erscheinung. Längs unserer Schnitte finden sie im freien Nordatlantik ihre Südgrenze bei etwa 20° N, wo sich Nord- und Südatlantisches Zentralwasser zusammenschließen. Die Gruppe umfaßt mehrere Verbreitungsmuster, das biantitropische, entweder auf Art- (Abb. 3–4) oder auf Gattungsebene (Abb. 5), und weitere auf eine der beiden Halbkugeln beschränkte Muster.

III. Die tropische Gruppe. Diese ist nicht nur die artenreichste, sondern weist auch die meisten Verbreitungsmuster auf. Beispiele werden gebracht für das mit Backus et al. (1970) als „broadly tropical" bezeichnete Verbreitungsbild, welches die nördlichen wie die südlichen Subtropen mit einschließt (Abb. 6–8) sowie für verschiedene, auf die eigentlichen Tropen beschränkte Muster. Tropische Arten können sowohl latitudinal (Abb. 9) wie longitudinal verbreitet sein, wobei sich die longitudinale Verbreitung auf die östliche Seite des Ozeans („guineisch", Abb. 10) oder die westliche („amazonisch", Abb. 11) ganz oder vorwiegend beschränken kann. Daneben gibt es offensichtlich eine Anzahl spezieller Verbreitungsmuster, von denen hier je ein Beispiel für ein pseudozeanisches Verbreitungsmuster (Abb. 10, *Polyipnus*) und ein auf das Südatlantische Zentralwasser bis zur südlichen Subtropischen Konvergenz übergreifendes Verbreitungsbild (Abb. 12) gegeben werden. Schließlich wird ein als „Agulhas pattern" bezeichnetes Verbreitungsmuster erörtert (Abb. 5, 13), welches von aus dem Indischen Ozean verdrifteten Fischen, vermutlich nur temporär, gebildet wird, da die expatrierten Tiere offenbar nur ausnahmsweise im Atlantik überleben können.

IV. Die Südgruppe. Bei den von uns im Gebiet der südlichen Subtropischen Konvergenz angetroffenen Fischen handelt es sich um Angehörige mehrerer Faunengemeinschaften. Beispiele für ein besonderes Verbreitungsbild, das Konvergenzmuster, werden gezeigt (Abb. 4, *Diaphus ostenfeldi*, und 14), charakteristische Vertreter der beiden weiteren Gruppen, Arten der Westwinddrift und der im weiteren Sinne antarktischen Fauna, werden erwähnt.

V. Die bathypelagische Gruppe. Von den etwa 80 von uns nur in Hols unterhalb 800 m gefangenen Fischen sind erst wenige hinsichtlich ihres geographischen Verbreitungsbildes untersucht. Trotz eines im Vergleich zu den mesopelagischen Fischen oft wesentlich größeren Areals scheinen auch die bathypelagischen Fische eher artspezifischen als globalen Verbreitungsmustern zu folgen. Ein solches Muster, vorläufig als „Nordatlantische Tiefenwasser-Verbreitung" bezeichnet, wird vorgestellt (Abb. 15).

Table 1

"Walther Herwig" transect 1966

Distribution of fish species (upper figures) and specimens (lower figures) according to station and depth

Latitude	35°N								20°N					0°					25°N					Tot.No of specimens	No.of hauls
Station	174	175	176	177	178	179	180a	180b	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197		
depth(m)																											
100	20 / 474										54 / 3838						25 / 398		50 / 1010	33 / 1559	40 / 2612					9891	6
200						45 / 672	57 / 872	73 / 1013	68 / 3080	68 / 800		72 / 738	73 / 754	74 / 842	75 / 1119	54 / 903						57 / 819	53 / 817	56 / 1275	61 / 4593	6028	7
300		20 / 250	31 / 450	70 / 1135	56 / 653									1	1			55 / 503								15242	12
400																											
500																											
600																											
700																											
minutes*) fished	60	75	75	75	80	90	65	90	90	75	43	80	80	75	80	80	60	120	70	80	70	110	110	105	105	31161	25
																										350 species	

*) time for shooting and hauling excluded

step hauls, depth range fished

"Walther Herwig" transect 1968

Distribution of fish species (upper figures) and specimens (lower figures) according to station and depth

Latitude	35°N				20°N					0°					25°S										Tot.No.of specimens	No.of hauls
Station	1	2	3	4	5	6	7	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
depth(m) 100	4 / 40					37 / 941			20 / 254				32 / 706	38 / 510				11 / 65	2 / 3						2 / 4					2523	8
200	11 / 63	8 / 150	15 / 102	30 / 134					64 / 667	43 / 185	44 / 381	48 / 232	63 / 617	51 / 462			15 / 56	29 / 182	16 / 110		18 / 112	23 / 190	6 / 9	5 / 11		22 / 131	19 / 183	11 / 87		4064	20
300							34 / 160	34 / 222		60 / 443							57 / 516				26 / 108			27 / 163				30 / 207		1819	7
400	16 / 169	13 / 149	16 / 37	16 / 51			36 / 262	35 / 235														36 / 476			33 / 132	37 / 391				1902	9
500																														-	-
600		24 / 150	31 / 131	29 / 149				76 / 625	104 / 996	79 / 778		73 / 751	78 / 646	72 / 617			67 / 548	53 / 408	40 / 212		44 / 265	47 / 333		50 / 268	58 / 345	64 / 589			64 / 655		8466	18
700																														-	-
800					52 / 308																									308	1
900																															
1000						52 / 416																								416	1
1100 - 1800																															
1900																															
2000							88 / 2947			117 / 940					95 / 423	85**) / 402				43 / 170			61 / 363				80 / 1039		70 / 591	6875	8
Tot.No.of species	20	25	42	46	52	75	102	102	126	104	125	88	97	90	95	85	83	57	47	43	53	65	62	58	67	76	83	73	70	426 species	72
Tot.No.of specimens	272	449	270	334	308	1357	3369	1082	1917	1406	1321	983	1969	1589	423	402	1120	655	325	170	485	999	372	442	481	1111	1222	949	591	26373	
minutes fished *)	60	60	60	60	30	45	90	60	60	60	30	45	60	60	30	30	60	60	60	30	60	60	45	60	60	60	45	60	60		

*) time for shooting and hauling excluded. **) in day light.

Table 3

"Walther Herwig" transect 1971/1 (Mar del Plata–Cape Town)

Distribution of fish species (upper figures) and specimens (lower figures) according to station and depth

Station	348	350	354	358	363	367	371	376	380	384	395	399	402	406	409	412	417	419	423	Tot.No.of specimens	No.of hauls
depth(m)							17 / 159					11 / 230				2 / 7			31 / 356	752	4
100		32 / 314	33 / 492	13 / 113	24 / 1292		35 / 290		11 / 551				13 / 184		32 / 660			47 / 791		4687	9
200		36 / 817		26 / 538					29 / 753											2108	3
300					47 / 668							10 / 54	29 / 803					61 / 668	42 / 416	2609	5
400																				-	-
500																			76 / 443	443	1
600		56 / 708					72 / 425		64 / 1164											2297	3
700					61 / 713										67 / 633					1346	2
800													57 / 560							560	1
900																				-	-
1000	43 / 998			68 / 665																1663	2
1100																					
1200																					
1300																					
1400																					
1500																	72 / 525			525	1
1600																					
1700																					
1800											66 / 475									475	1
1900			69 / 1273			71 / 1572		94 / 1193		48 / 149			68 / 839							5026	5
2000																					
2100																					
2200																79 / 526				526	1
Tot.No.of species	43	71	79	75	72	71	85	94	71	48	66	15	63	68	79	80	72	77	86	265 species	38 hauls
Tot.No.of specimens	998	1839	1765	1316	2673	1572	874	1193	2468	149	475	284	1537	839	1293	533	525	1459	1215	23017	
minutes fished	15	60	45	45	45	60	45	90	45	30	120	30	45	90	30	105	60	30	45		

Table 4

"Walther Herwig" transect 1971/2 (Cape Town–Madeira)

Distribution of fish species (upper figures) and specimens (lower figures) according to station and depth

Latitude	25°S												0°						20°N				Tot.No.	No.of
Station	427	431	435	439	443	447	451	455	459	463	467	471	478	482	486	490	494	498	502	506	510	512	specim.	hauls
depth(m)						13 / 83																	1760	3
100		19 / 696		23 / 715				19 / 654		23 / 1436		33 / 1023		63 / 904		53 / 880		59 / 1183					5814	6
200														64 / 542									2080	4
300		49 / 476		43 / 328		46 / 274		54 / 404		63 / 456		66 / 906						71 / 806					2112	4
400																							-	-
500		67 / 468																					3574	4
600										91 / 1177		99 / 883				94 / 1156		103 / 1067					1177	1
700				68 / 522		63 / 476								114 / 1096									2094	3
800																							-	-
900								93 / 821															821	1
1000																							-	-
1100																							-	-
1200																							-	-
1300															121 / 1329								1329	1
1400																							-	-
1500																							-	-
1600																							-	-
1700																							-	-
1800																							-	-
1900							111 / 898		87 / 484		115 / 983						127 / 968				74 / 631		3964	5
2000	90 / 625		99 / 538		104 / 624								127 / 1286						116 / 754	102 / 667		86 / 825	3409	5
2100																							1910	2
Tot.No. species	90	88	99	86	104	77	111	111	87	106	115	116	127	135	121	107	127	129	116	102	74	86	424 species	39
Tot.No. specim.	625	1640	538	1565	624	833	898	1879	484	3069	983	2812	1286	2515	1329	2036	968	3056	754	667	631	825	30017	
Minutes fished	60	45	60	45	60	45	60	45	60	45	60	50	60	45	60	30	60	45	60	60	60	60		

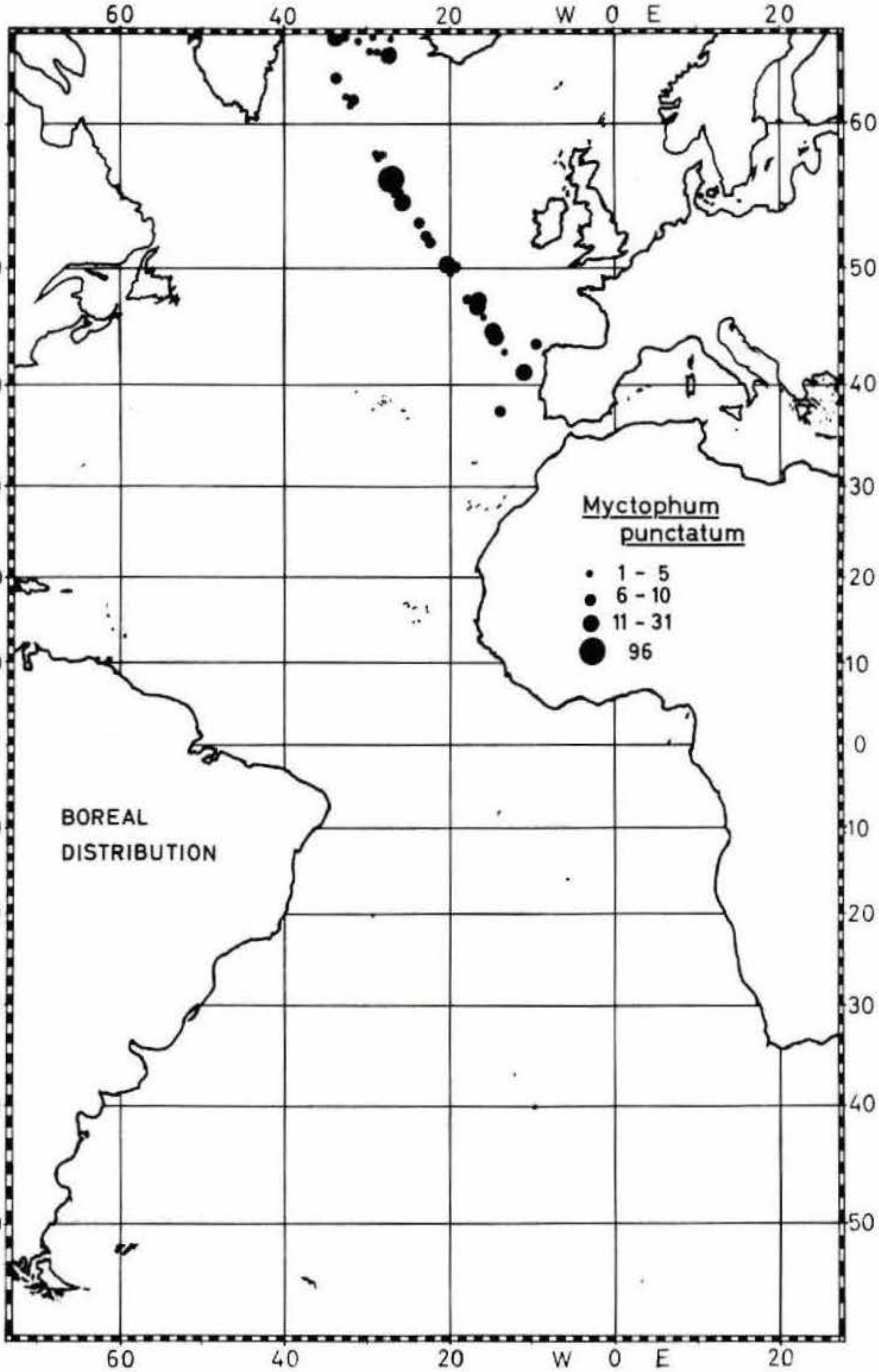

Fig. 2

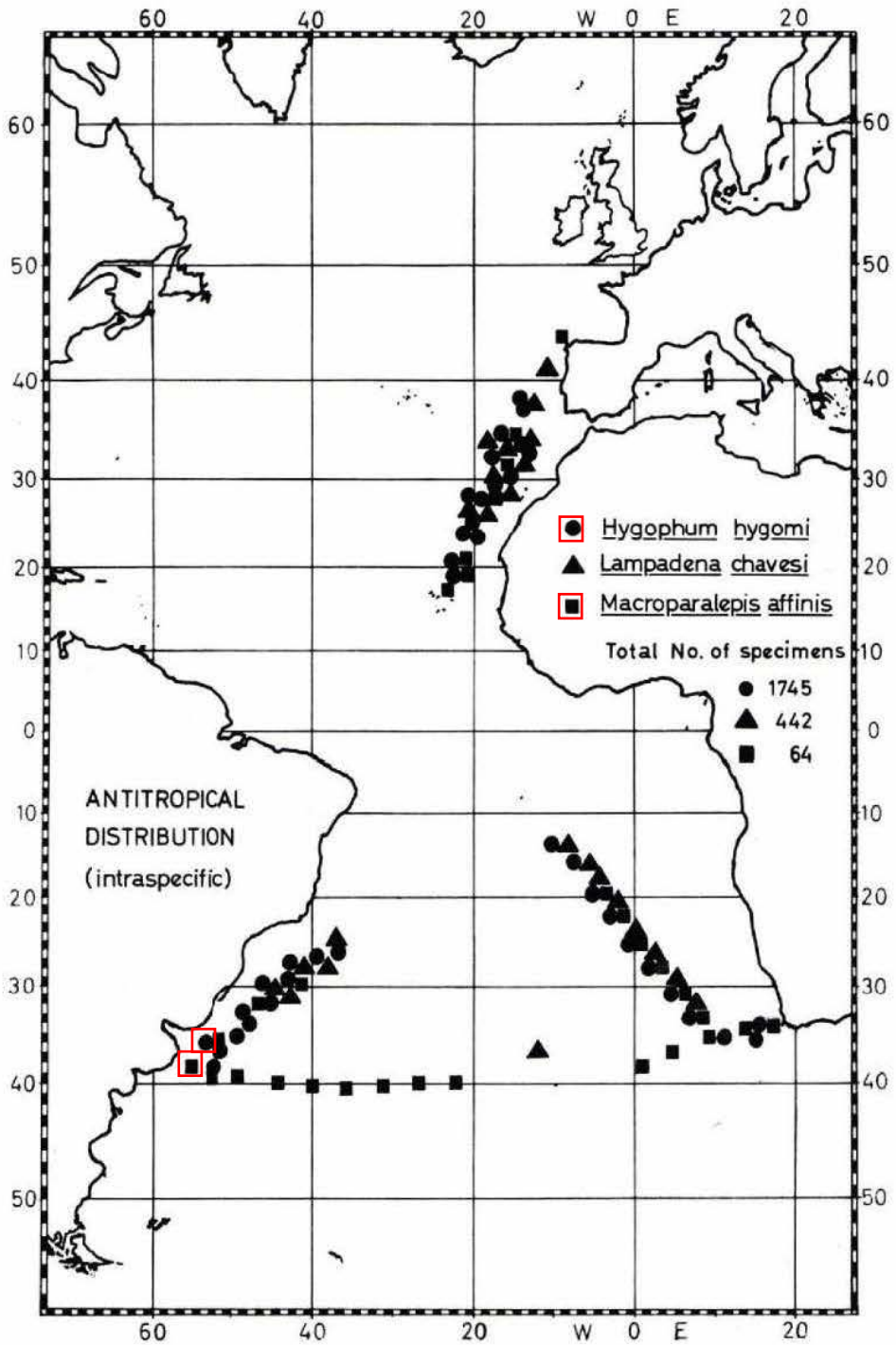

Fig. 3

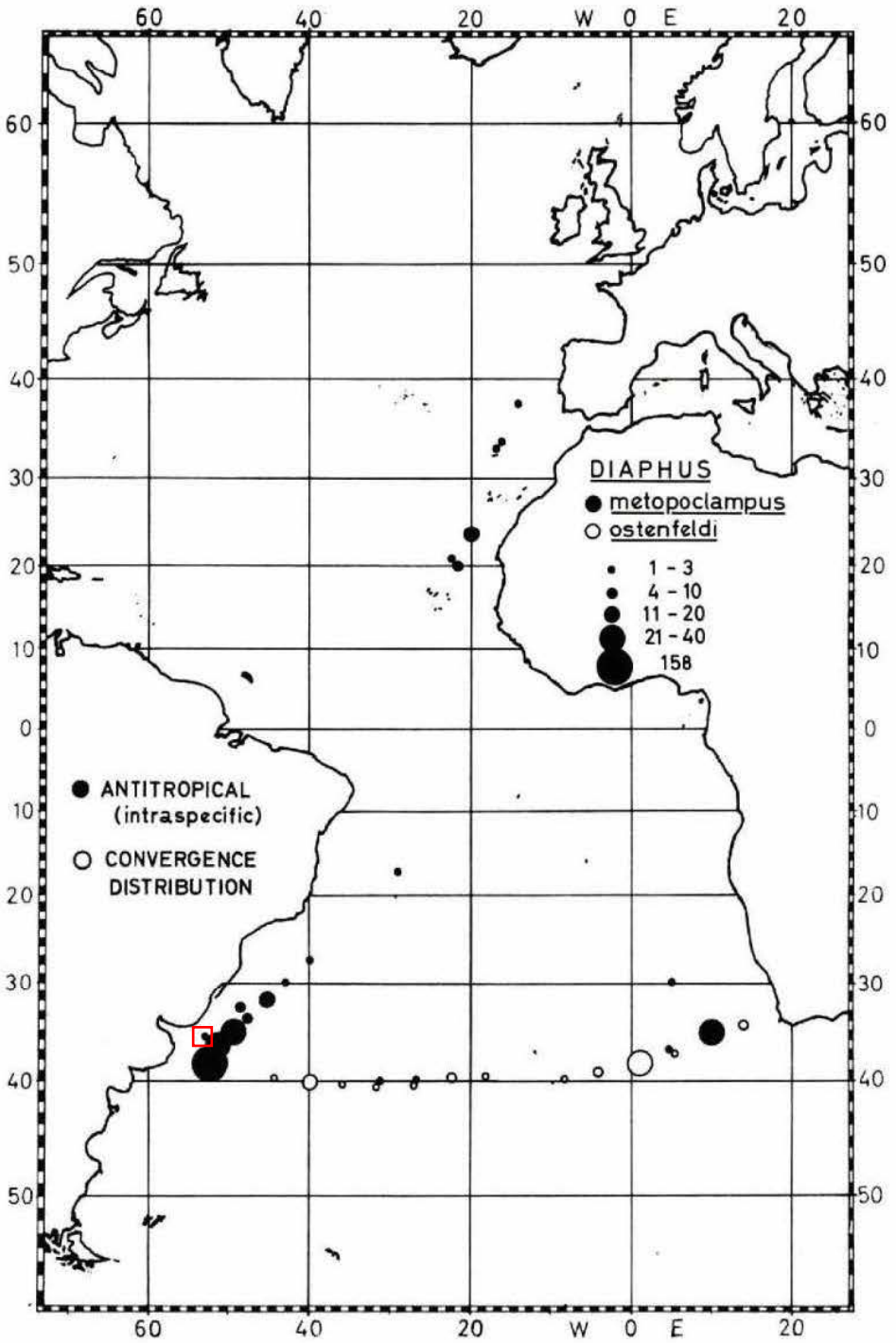

Fig. 4

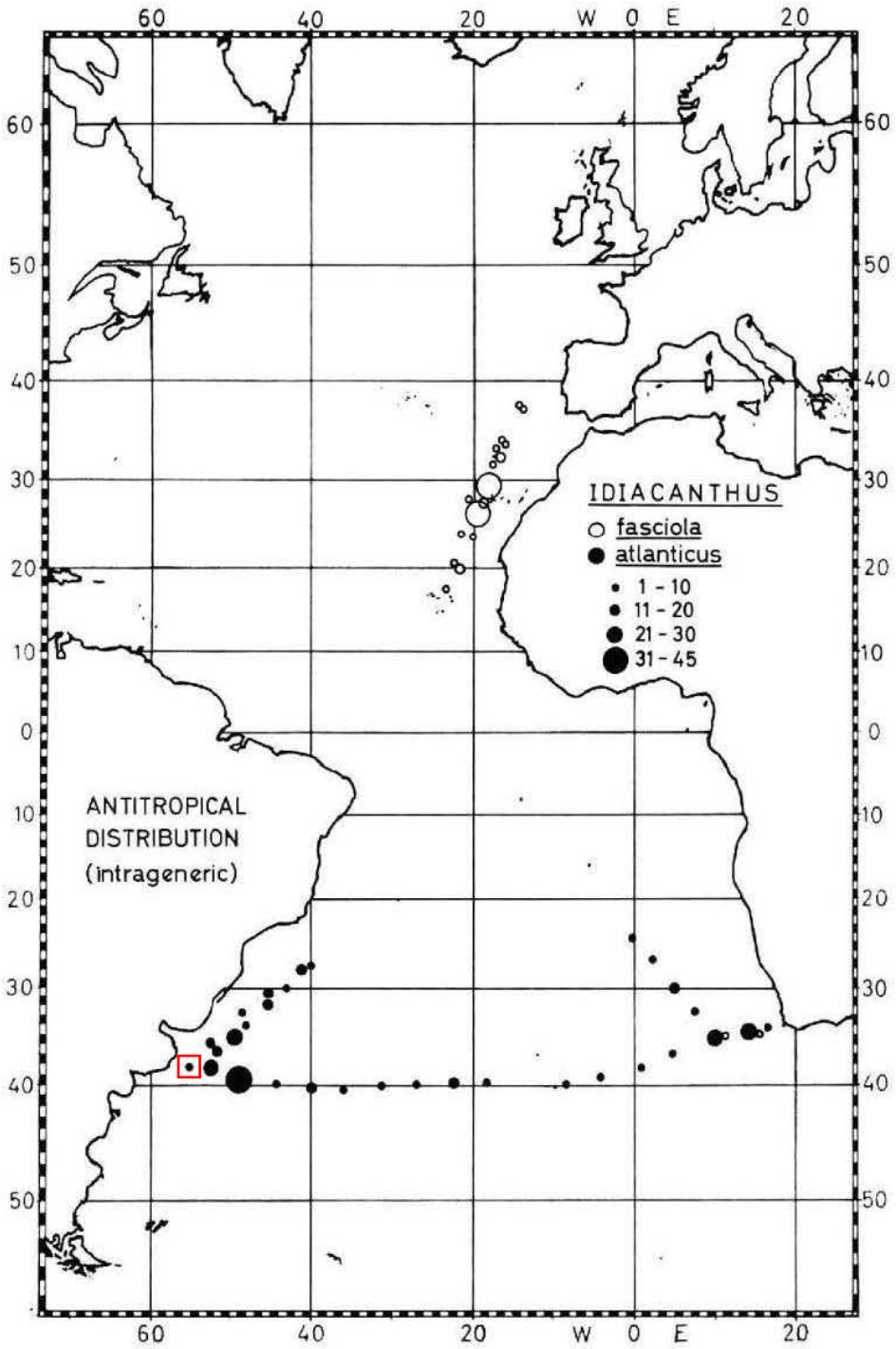

Fig. 5

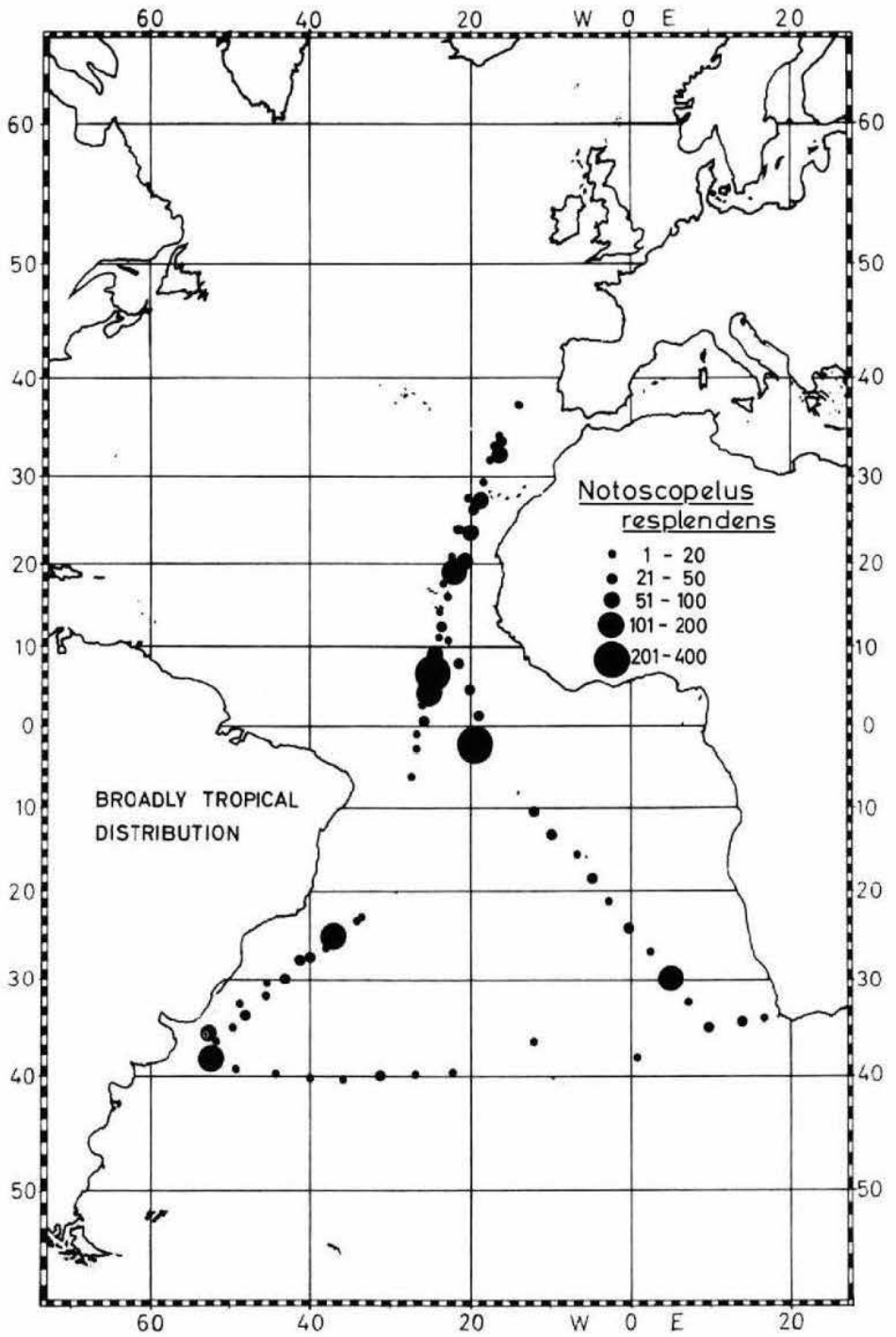

Fig. 6

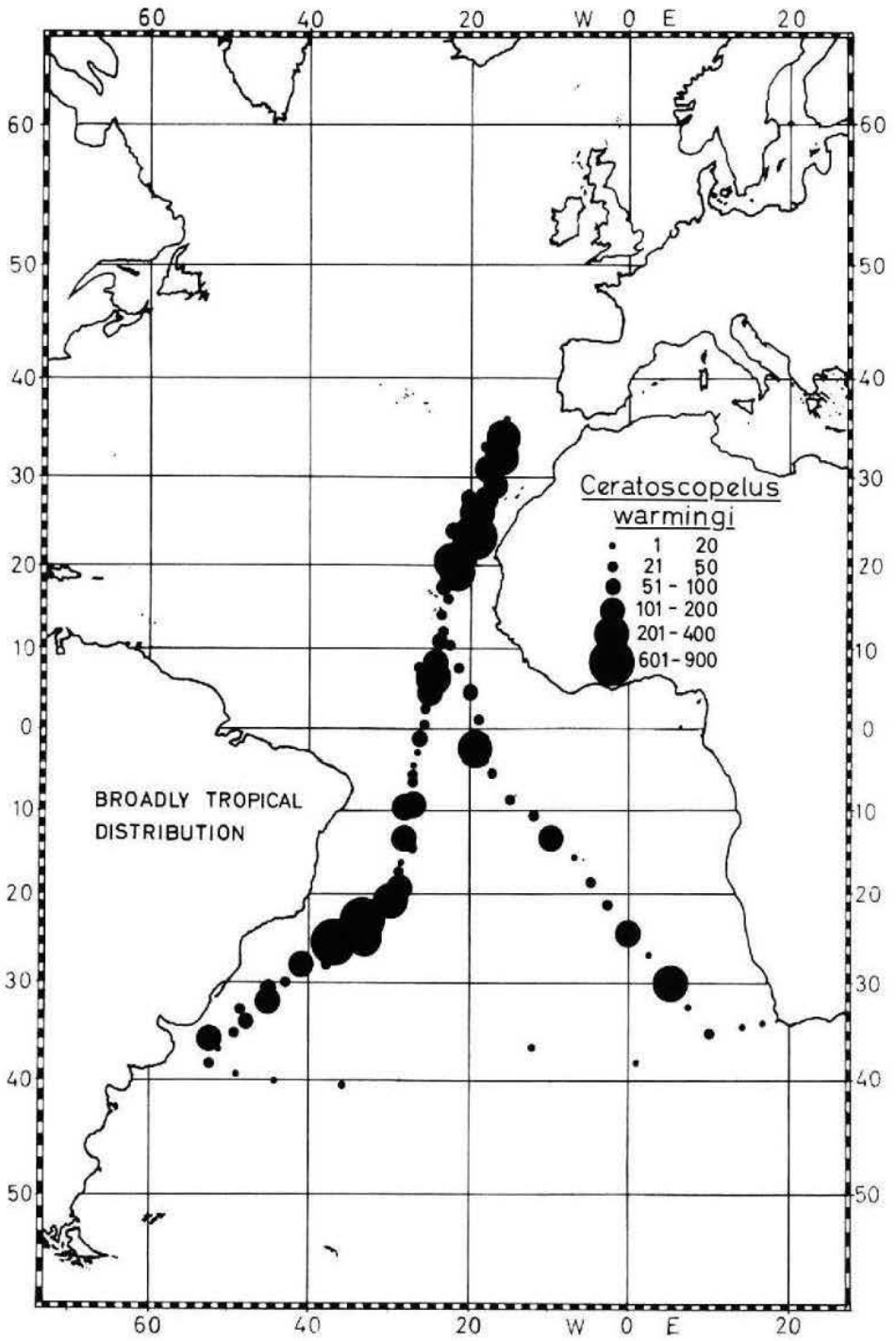

Fig. 7

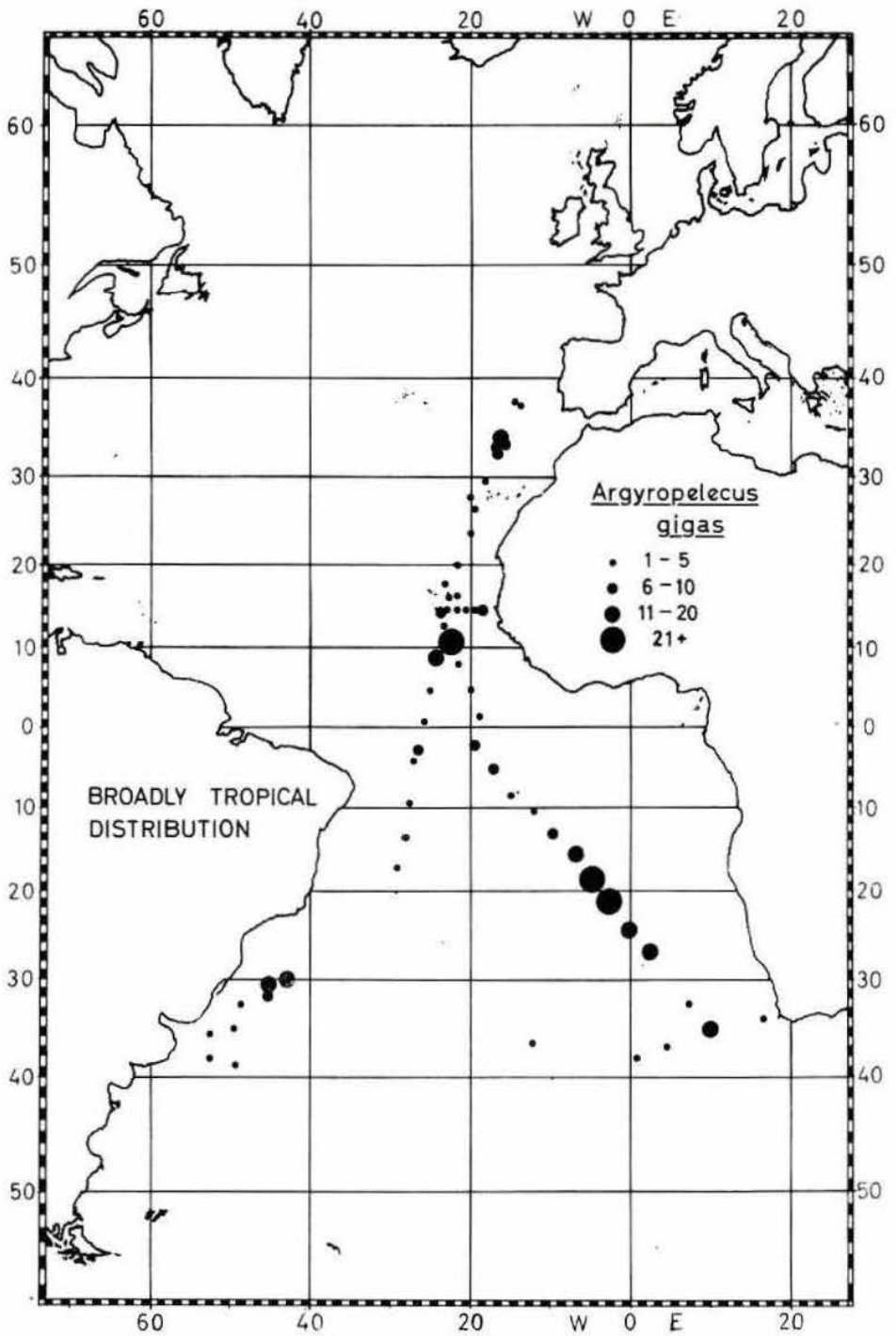

Fig. 8

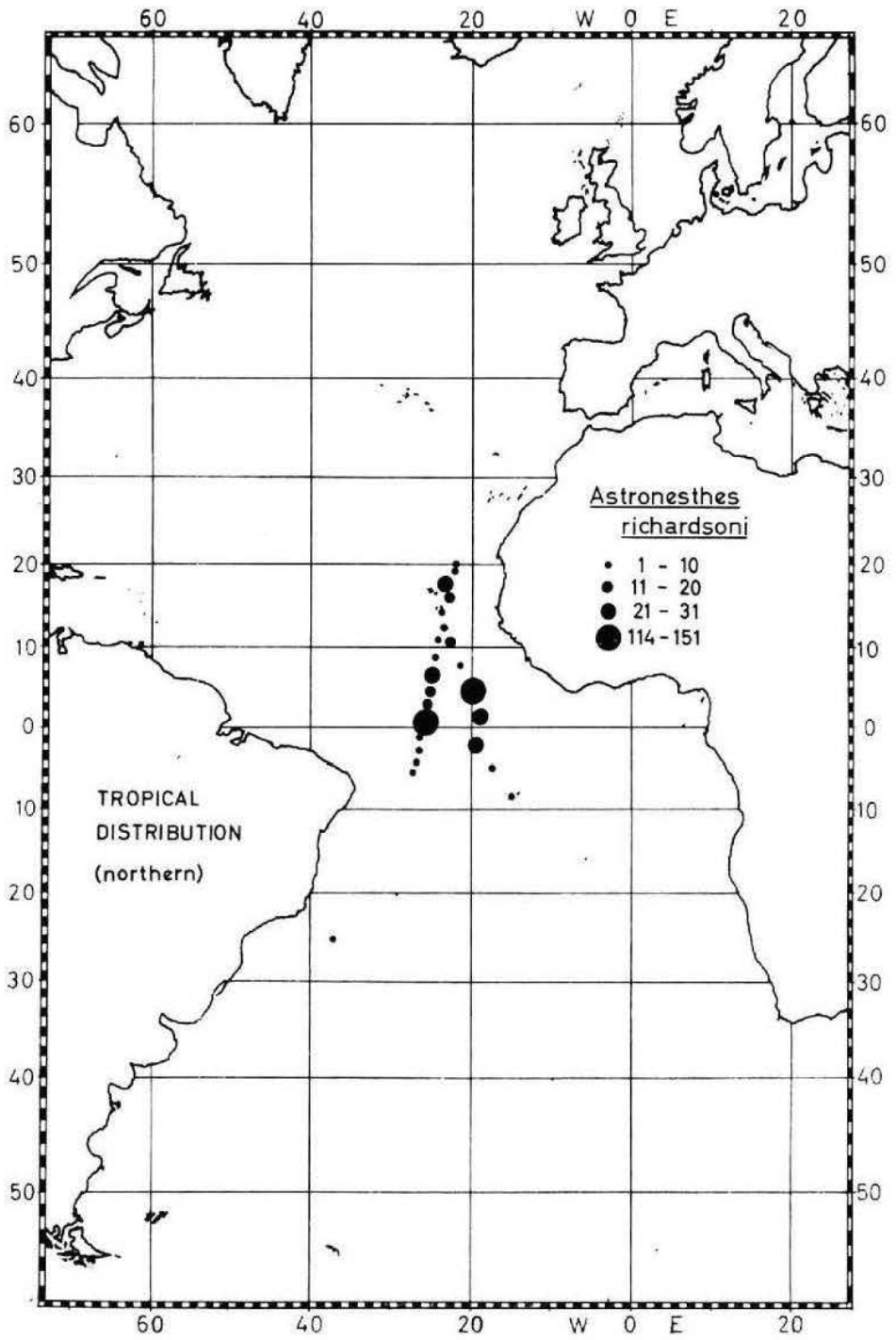

Fig. 9

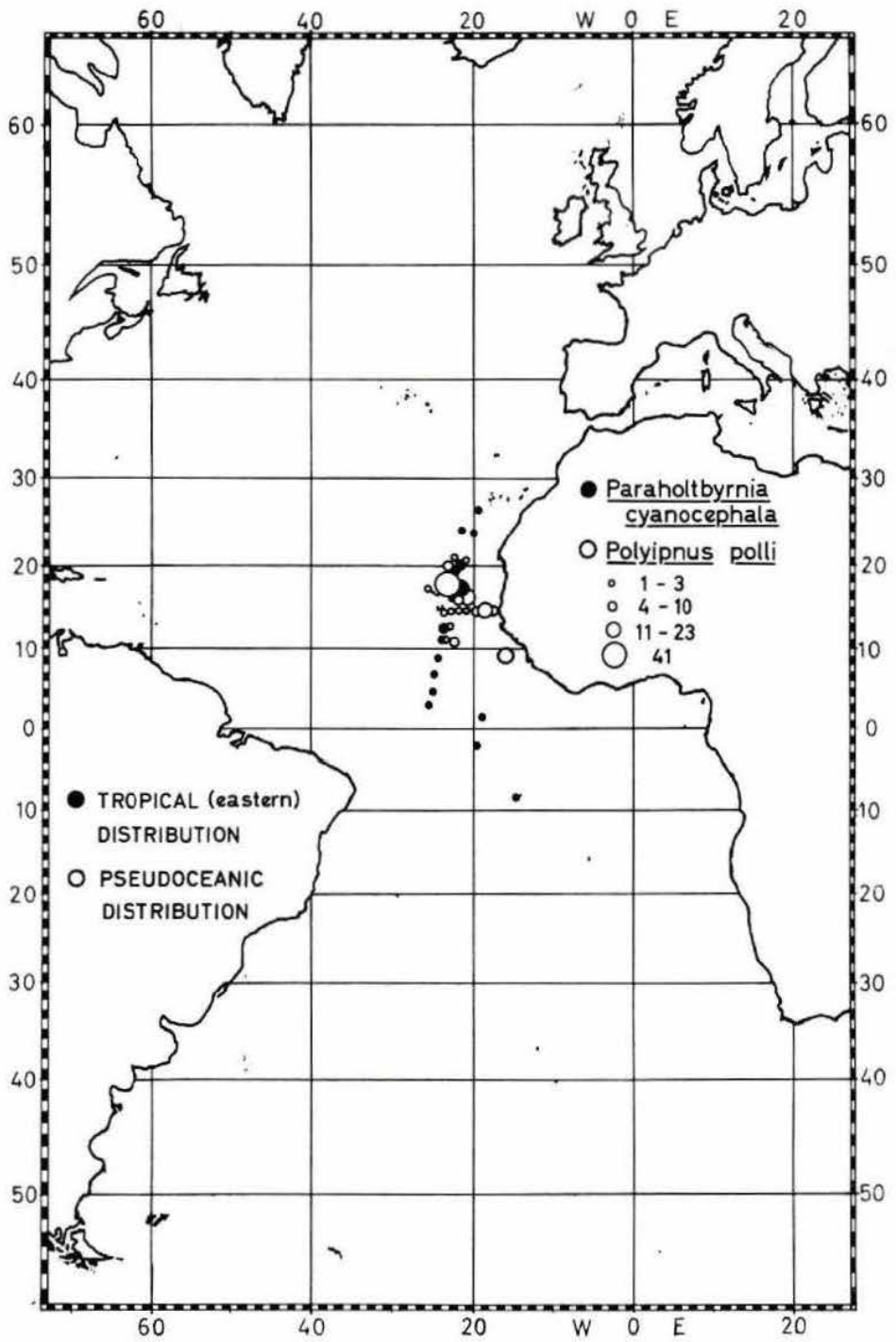

Fig. 10

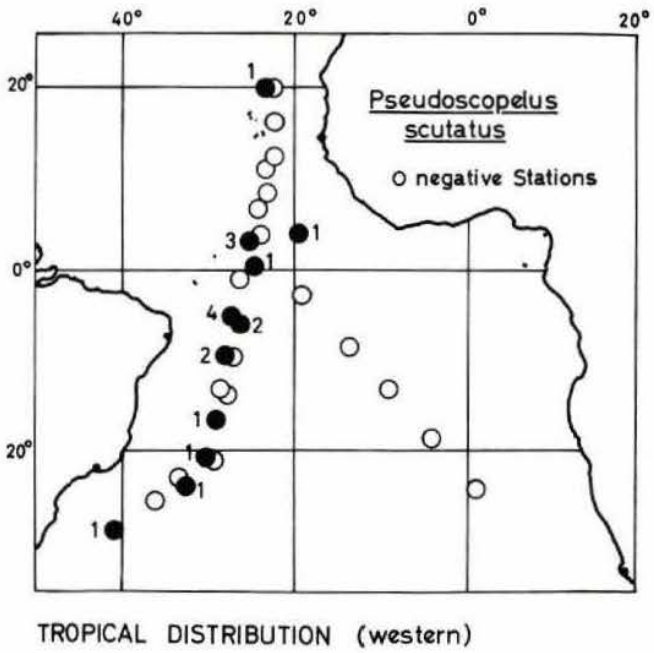

Fig. 11. Figures refer to numbers of specimens (From KREFFT, G., 1971, Arch.Fisch.Wiss. **22**, 165–174, Abb. 9)

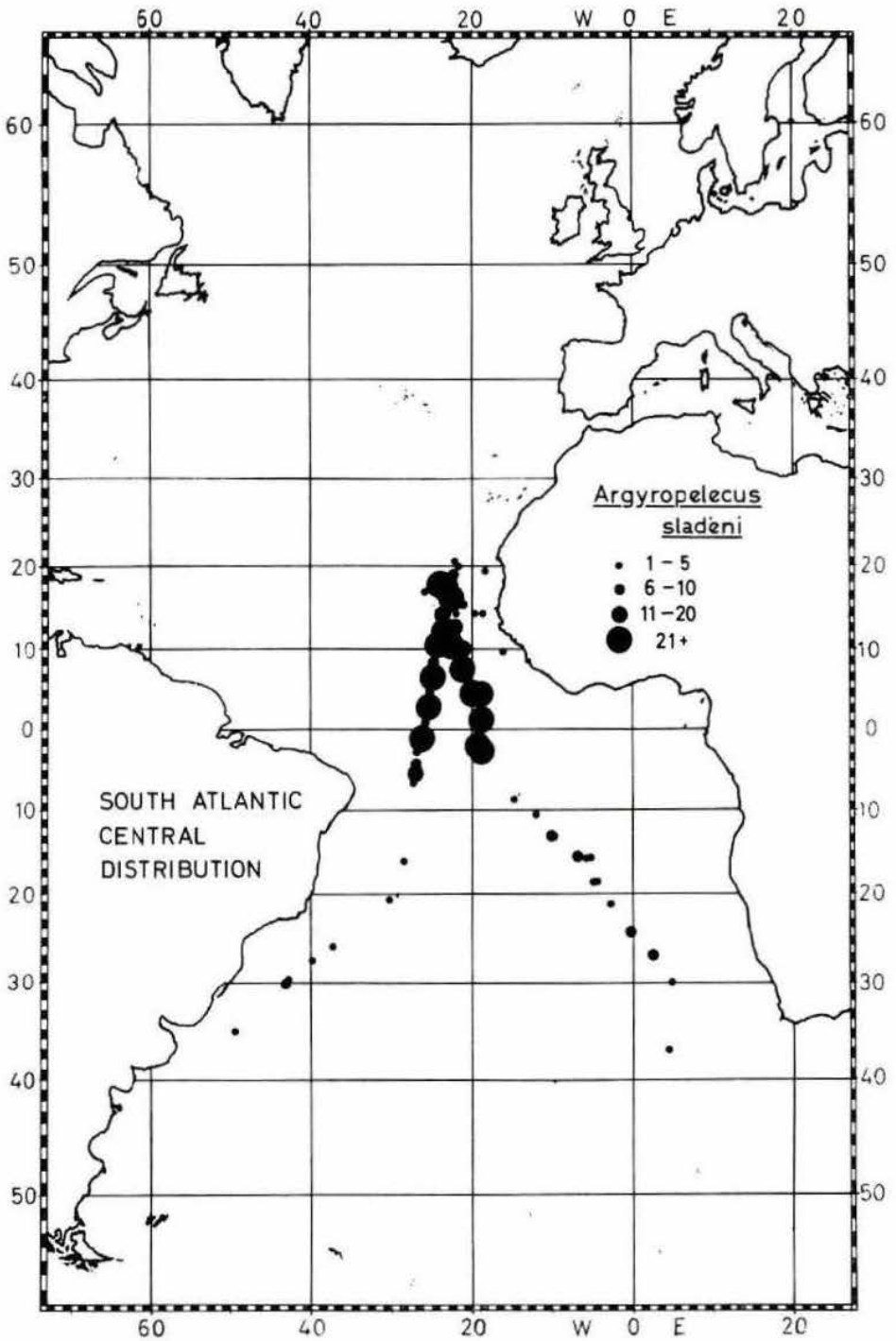

Fig. 12

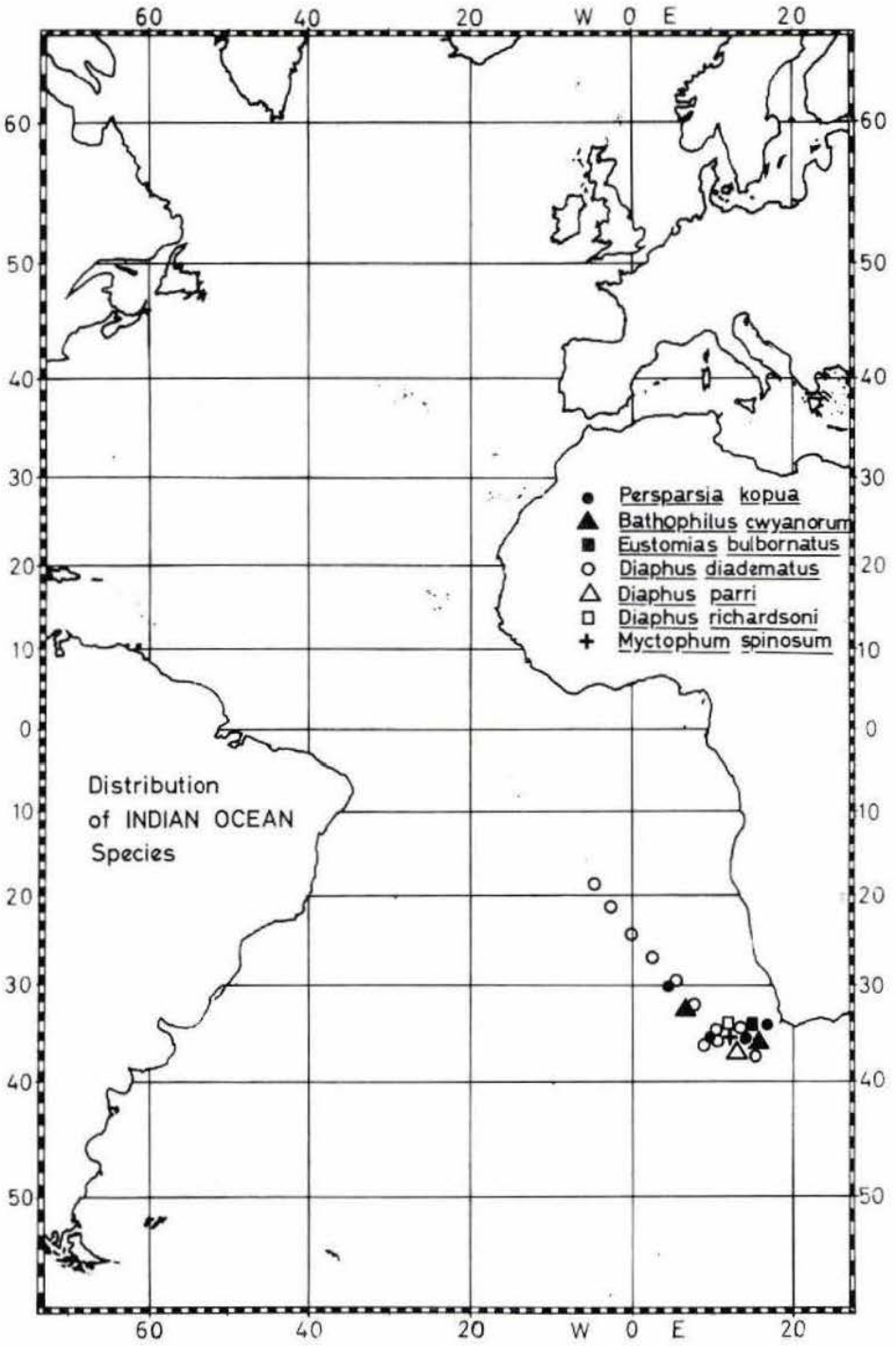

Fig. 13

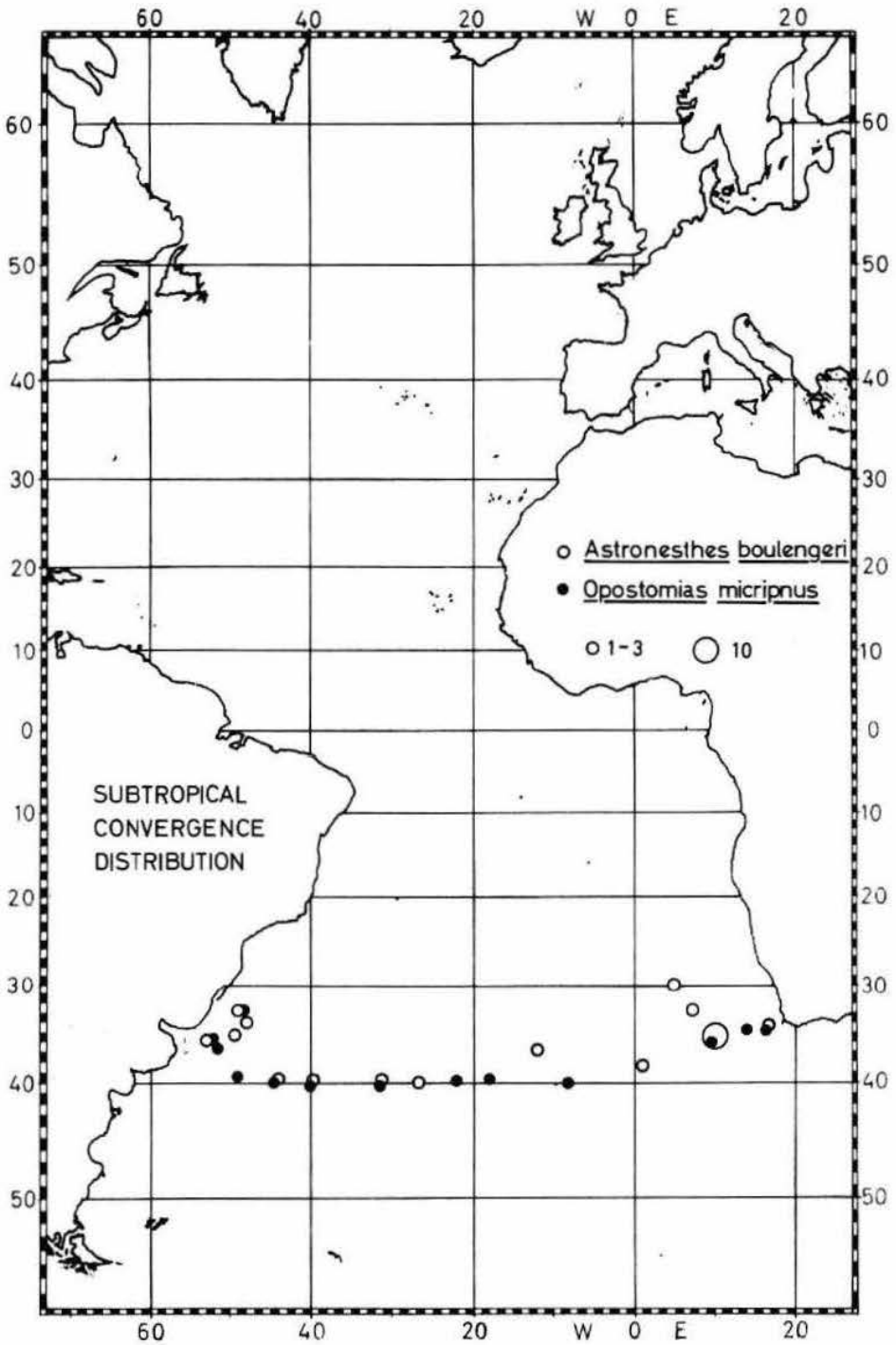

Fig. 14

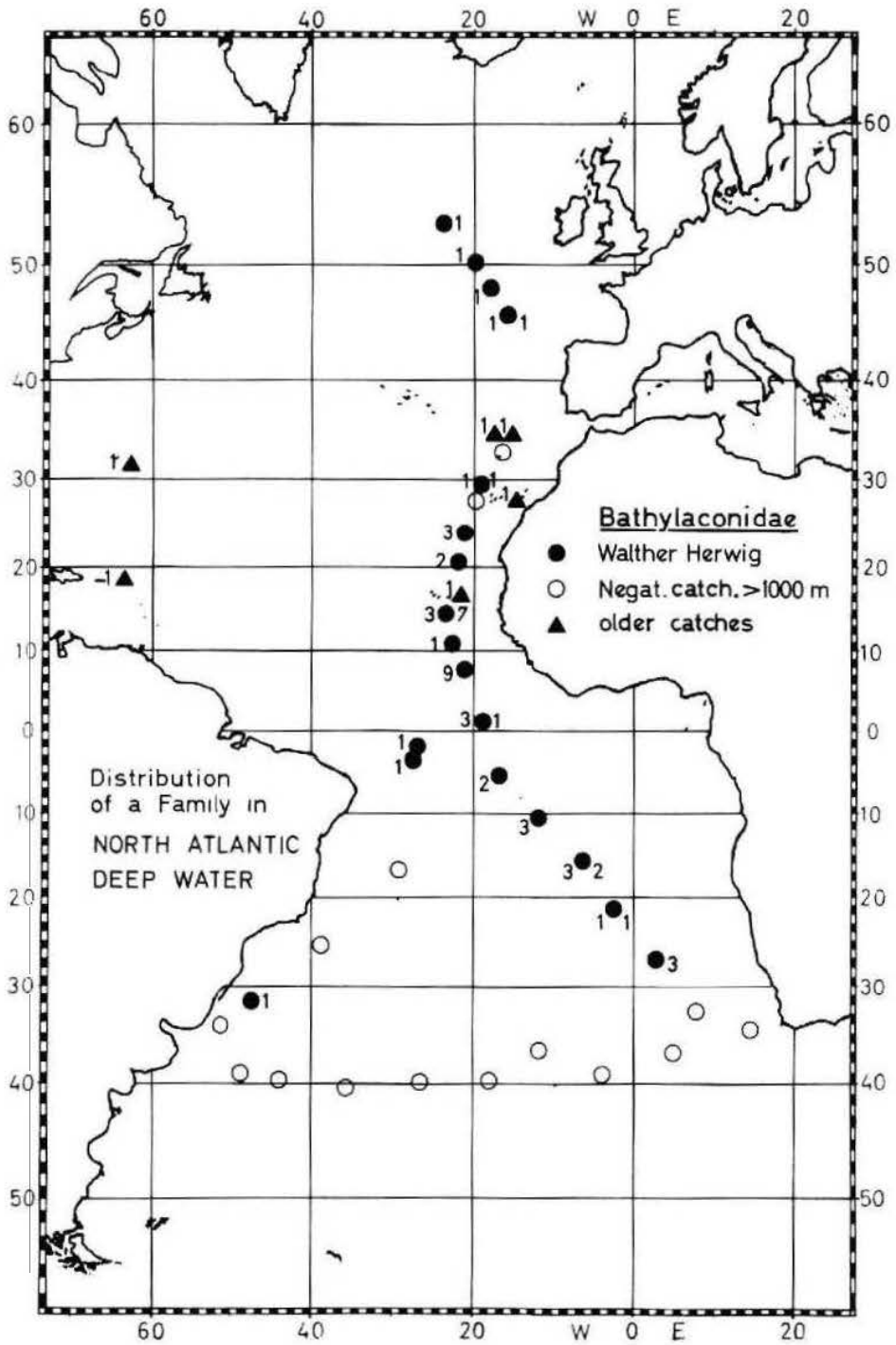

Fig. 15. Numbers of specimens given by figures, *Bathylaco* left, *Herwigia* right of the stations

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