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# Vertical Zones and Formation of the Parasitic Fauna in Deepwater Fishes from the Off-shore Areas of the North Atlantic

by

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## ABSTRACT

Eight groups of parasites (epicontinental, epipelagic, mesopelagic, mesobenthic, bathybenthic, bathypelagic, bathyal-pelagic, polyzonal) are defined in accord with the vertical zones of the ocean. It is concluded that most of the typical deepwater parasites are not closely related to certain depths. As for the meso-, bathy- and bathyal-pelagic fishes, the ranges of their specific deepwater parasites coincide to some extent with those of their hosts. The ranges of specific deepwater parasites in fishes ecologically related to the bottom are smaller than the ranges of their hosts. The parasitic fauna of some fishes is stated to get poorer with depth at the expense of secondary deepwater forms and polyzonal species. The number of ancient deepwater parasite species does not decline with depth and only the reduction in the incidence and degree of infestation is observed.

## INTRODUCTION

Comprehension of the fish parasite circulation, estimation of the factors affecting their distribution, determination of their position and role in deepwater biocenoses - these are the problems of theoretical and practical concern however very poorly studied.

Manter (Manter, 1934, 1955) was the first to study the peculiarities in the distribution of marine fish parasites, exemplified by Trematoda, in relation to depth. On analysing 80 fish species captured from 80 to 1060 m depths at the coast of Florida, he found out that most of the trematodes were dwelling mainly in the upper layers, some species - at great depths and only few of them were observed within a wide depth range without showing their broad specificity. Manter also pointed to the trematode fauna diversity decreasing with depth and many parasites in deepwater fishes having a wide circle of hosts.

The scantiness of parasitic fauna (one species of parasitic copepod found) was typical for some Pacific bathypelagic fishes such as Cyclothone microdon, C. pallida, Gonostoma witjasi, Lampanictus nannochir laticauda, Chauliodes sp. captured from the 800 to 5720 m depths (Gusev, 1958). At the same time 8 species of parasites were found in Macrurus (Coryphaenoides) acrolepis dwelling at great depths however in the near-bottom layer.

While discussing these findings, Yu. I. Polyansky (Polyansky, 1958) expressed the opinion that the formation of deepwater parasitic fauna is determined by a number of factors including the temperature regime, the reduced composition of the intermediate host fauna, possibly, the physical effect of pressure and, to a high degree, food composition. This idea is, to some extent, corroborated by the subsequent investigations. In particular, the low percentage of infested fish is accounted for by peculiarities in feeding and by the distance from fishes to the bottom and to the surface (Orias et al., 1978; Zubchenko, 1979). It is stated that the qualitative and quantitative composition of parasitic fauna depends on the food spectrum of hosts (Campbell et al., 1980), that formation of parasite populations depends on the density of fish populations and their trophic relationship (Noble, 1966), that near-bottom fishes are infested more heavily than those dwelling in water mass (Noble, 1973; Campbell et al., 1980;

Mauchline, Gordon, 1984). The conclusion is drawn that high pressure and low temperature do not hinder the development of parasitism (Noble, 1966; Noble E., Noble G., 1978).

## MATERIAL AND METHODS

The distribution patterns of 224 parasite species (Myxosporidia - 34, Ciliata - 4, Monogenea - 25, Gyrocotylidea - 1, Cestoda - 28, Trematoda - 72, Nematoda - 14, Acanthocephala - 5, Hirudinea - 4, parasitic copepods - 37 species) found in 2,769 fishes belonging to 81 species from 42 families are analysed. Fish were taken from 100 to 2200 m depths in the off-shore areas of the North Atlantic: in the east - on the Outer Bailey's, Bill Bailey's, George Bligh, Rockall, Porcupine and Hatton Banks, in the central areas - on the Reykjanes Ridge and North Atlantic Ridge from the continental slope of Iceland to the Azores, and in the west - off the Baffin Island and Davis Strait, Labrador Peninsula, Flemish Cap and Orphan Banks and the Grand Bank of Newfoundland.

## RESULTS

The analysis of obtained and historic data shows that fish parasites from the off-shore areas of the North Atlantic may be divided into several groups corresponding to vertical zones of the ocean. The zones are designated after T.S. Rass (Rass, 1967).

Epicontinental species. We found them at the depths up to 800 m in Squalus acanthias, Raja radiata, R. undulata, Conger conger, Brosme brosme, Gadus morhua morhua, G. morhua ogac, Melanogrammus aeglefinus, Molva molva, Pollachius pollachius, Zeus faber, Anthias anthias, Pagellus acarne, Antigonia capros, Anarhichas denticulatus, A. lupus, A. minor, Eutrigla gurnardus, Myoxocephalus scorpius, Cyclopterus lumpus, Hippoglossoides platessoides platessoides, Pleuronectes platessa, Solea vulgaris, Lophius piscatorius. Epicontinental species are as follows: Myxidium oviforme, Myxoproteus elongatus, Ceratomyxa appendiculata, Chloromyxum leydigi, Trichodina cottidarum, T. domerguei subsp. saintjonsi, T. murmanica, Tripartiella sp., Gyrodactylus grönlandicus, G, marinus, G. pterigialis, Calicotyle kröeri, Erpocotyle laevis, Squalonchocotyle abbreviata, Diclidophora denticulata, Plectanocotyle gurnardi, Fistulicola dalmatinus, Abothrium gadi, Pyramicocephalus phocarum, Echinobothrium raji, Sphyriocephalus tergestinus, Lacistorhynchus tennuis, Pterobothrium lintoni, Anthobothrium cornucopia, Echeneibothrium variabile, E. fallax, Phyllobothrium lactuca, Ph. minutum, Ph. tridax, Trilocularia acanthiae-vulgaris, Aporocotyle simplex, Fellodistomum fellis, Steringophorus agnotus, Steringotrema ovacutum, Zoogonoides viviparus, Diphterostomum microacetabulum, Deretrema pycnorganum, Lepidophyllum steenstrupii, Lepidapedon microcotyleum, Acanthopsolus anarrhichae, Opechona bacillaris, Helicometra indica, Plagioporus idoneus, Podocotyle atomon, Prosorhynchus squamatus, Bucephaloides gracilescens, Derogenes crassus, Lecithohirium rufoviridae, Brachyphallus crenatus, Adinosoma gaewskaye, Pseudanisakis tricupola, Cucullanus cirratus, C. hians, Ascarophis morrhuae, Malmiana brunnea, M. scorpii, Johansonia arctica, Platybdella anarrhichae, Sarcotaces arcticus, Chondracanthus lophii, Acanthochondria cornuta, Lernentoma asellina, Caligus curtus, C. elongatus, Lepeophteirus pollachii, Dinemoura producta, Eudactylina acanthii, Lernaeocera branchialis, Charopinus dalmanni, Schistobrachia ramosa, Dendrapta cameroni, Lernaeopodina longimana, Lernaeopoda galei, Clavellodes rugosa. A low infestation of hosts shows that these parasites are not typical for the off-shore areas of the North Atlantic and they occur there occasionally. This is confirmed by the fact that none of these species was found both in ancient and secondary deepwater fishes.

Epipelagic species. They are not numerous and may be found in Mallotus villosus villosus, Boreogadus saida, Micromesistius poutassou, Regalecus glesne, Caranx ronchus, Trachurus trachurus, Brama brama, Coryphaena hippurus, Scomber scombrus mainly at the depths up to 600 m. This group includes Sphaeromyxa hellandi , Myxobolus aeglefini, Diclidophora minor, Gymnorhynchus gigas, G.horridus, Pelichnibothrium speciosum l., Tetrochetus mitenevi, Opechona orientalis, Anisorchis opisthorchis, Hemiurus communis, Lecitaster confusus, Corynosoma strumosum l., Bolbosoma vasculosum l. These parasites are not found in deep-water fishes, though sometimes their hosts bring them into meso- and bathy-pelagial (Sphaeromyxa hellandi, Myxobolus aeglefini, Diclidophora minor, Corynosoma strumosum l. and some others). Once Bolbosoma vasculosum l. was registered at the 800-1250 m depths. In this case we can only speak of an occasional penetration of some parasites from epicontinental and epipelagic groups into adjacent deepwater layers.

Mesopelagic species. They are found mainly at the 200 to 800 m depths in Hexanchus griseus, Maurolicus muelleri, Chauliodus spp., Alepisaurus ferox, Lampadena speculidera, Notolepis rissoi, Nemichthys scolopaceus, Trachipterus arcticus, Ruvettus pretiosus, Helicolenus dactylopterus, Sebastes marinus, S. mentella. This group includes Myxidium incurvatum, Leptotheca macrospora, Protocotyle grisea, Mycrocotyle caudata, Gempylitrema longipedunculatum, Bothriocephalus scorpii, Hepatoxylon trichiuri, Phyllobothrium dohrnii, Otodistomum veliporum, Rhipidocotyle sp., Dinosoma tortum, Lecithophyllum bothriophoron, Cucullanus heterochrous, Ascarophis filiformis, Chondracanthus nodosus, Sagum sp., Peniculus clavatus, Sarcotretes eristaliformis, Sphyrion lumpi.

Mesobenthic species. These are found at the 400 to 1300 m depths in Argentina silus, Chimaera monstrosa, Onogadus argentatus, Urophycis chuss, Licodes esmarki, Glyptocephalus cynoglossus, Hippoglossus hippoglossus, Reinchardtius hippoglossoides. and are represented by Myxidium sphaericum, Zschokkella hildae, Ortholinea divergens, Schulmania aenigmatosa, S. quadrilobata, S.ovale, Ceratomyxa drepanopsettae, C.ramosa, Leptotheca simplex, Alataspora sp., Calicotyle affinis, Chimaericola leptogaster, Polipnicola argentinae, Gyrocotyle fimbriata, Steringophorus furciger, Steganoderma formosum, Lepidophyllum cameroni, Stephanostomum baccatum, Lepidapedon elongatum, L. rachion, Helicometra plovmornini, Podocotyle reflexa, Stenakron vetustum, S.quinquelobata, Spinoplagioporus minutus, Genolinea laticauda, Gonocerca crassa, G. macroformis, G. phycidis, Ascarophis arctica, Spinitectus cristatus, Capillaria kabatai, Diocus frigidus, Lepeophteirus hippoglossi, Hatschekia hippoglossi, Neobrachiella rostrata, Clavella pinguis. These two groups are transitive in a way. Some species belonging to them (Myxidium incurvatum, Leptotheca macrospora, Ceratomyxa drepanopsettae, Steringophorus furciger, Chondracanthus nodosus etc.) may be also found at shallower depths. Occurrence of the parasites from these groups at great depths may be related, as regards those with the direct life cycle, with the biology of hosts and for the parasites with the complicated life cycle with the distribution of intermediate hosts and low final host specificity. This is, as a rule, typical of the parasites in the secondary deepwater fishes. Penetration of elements from these groups into deeper layers is exemplified by infestation of bathial-pelagic fishes with Zschokkella hildae, Lepidapedon elongatum, L. rachion, Gonocerca crassa, Capillaria kabatai, Lecithophyllum bothriophoron.

Bathybenthic species. They were found in a wide depth range (400–1300 m) in Notacanthus nasus and Macrourus berglax. and include Zschokkella kudoi, Sinuolinea magna, Davisia newfoundlandia, Syncoelicotyle polyorchis, Cyclocotyloides pinguis, Atlanticotyle notacanthi, Antorchis spinosus, Clavellomimus macruri. This list of parasite species will probably be amplified in the course of further investigations.

Bathypelagic species. None of these were found probably because of few fish (3 spec. of Malacosteus niger) from the bathypelagic ichthyocene analysed. Besides, it seems to be one of the poorest groups of parasites. This conclusion may be drawn if we take into account the data of A.V.Gusev (Gusev, 1958) and Mauchline and Gordon (Mauchline and Gordon, 1984) who did not find helminths in the stomachs of pelagic fish from 0 to 2500 m depths.

Bathyal-pelagic species. These parasites dwell at 600 to 2200 m depths. During vertical migrations of hosts they ascend to upper (to 400 m) layers. These species are as follows: Myxidium melanocetum, M.melanostigmum, M. profundum, Myxidium sp., Ceratimyxa tenuispora, Leptotheca coelorhyncha, L.quadritaenia, Auerbachia anomala, Palliatus indecorus, Myxobolus lairdi, Trilospora minuta, Diclidophora attenuata, D.caudata, D. macruri, D.nezumia, Paracyclocotyle cherbonnieri, Choricotyle oregonensis, Probothriocephalus muelleri, Parabothriocephalus macruri, Philobythoides stunkardi, Paraccacladium jamiesoni, Steringophorus pritchardae, S. profundum, S.thulini, Olesonium turneri, Steganoderma abyssorum, Hudsonia agassizi, Lepidapedon luteum, Genitocotyle atlantica, Bathycreadium elongata, B. flexicolis, Bathycreadium sp., Podocotyle olssoni, Gonocerca macrouri, Glomericirrus macrouri, Dinosoma triangulata, Lecithophyllum anteroporum, Johnstonmawsonia sp., Euzetacanthus simplex, Sarcotaces komaii, Chondracanthodes radiatus, Lateracanthus qudripedis, Lophoura bouvieri, Periplexis lobodes, Neobrachiella sp., Neobranchia auriculata found in Alepocephalus bairdi, A. agassizi, Antimora rostrata, Mora moro, Lepidion eques, Trachyrhynchus trachyrhynchus, Trachonurus villosus, Coelorhynchus coelorhynchus, C.occa, Coryphaenoides rupestris, C. longifilis, C.armatus, Nezumia bairdi, Chalinura mediterranea, C.simula, C.brevibarbis, Coryburus sp., Beryx decadactylus, B. splendens, Epigonus telescopus, Aphanopus carbo. This group of parasites, in our opinion, is quite unique first and foremost because they adapted to rather a wide depth range (400-2200 m). Many bathyal-pelagic parasites show stringent specificty. With few exceptions, they have a narrow circle of hosts and are not found in fishes from other groups.It may be supposed that the 2200 m depth is not the limit of their distribution.

Polyzonal species. We believe it necessary to distinguish this group of parasites which includes such widespread species as Grillotia erinaceus l., Scolex pleuronectis l., Derogenes varicus, Hemiurus levinseni, Lecithaster gibbosus, Anisakis simplex l., Hysterothylacium aduncum, Pseudoterranova decipiens l., Echinorhynchus gadi, Clavella adunca. These parasites adapted to dwelling within a wide depth range (in our surveys they were found from 100 to 2200 m depths), but in contrast to bathyal-pelagic species they do not show stringent host specificity and are found in fish from different groups, i.e. they are widely spread not only horizontally but vertically as well.

DISCUSSION

Substantial levelling of numerous biotic and abiotic factors such as salinity, temperature, content of dissolved substances etc. at great depths diminishes noticeably their role in the formation of parasitic fauna in deepwater fishes in contrast to comparatively shallow shelf zones where these factors affect greatly the distribution of parasites. Moreover, it turned out that even a high stenothermic degree of deepwater fishes (Ekman, 1953) does not hinder the vertical distribution of deepwater parasites including those with the complicated life cycle.

Though typical deepwater parasites were absent from the zone above the thermocline (300-400 m), most of them do not exhibit strict correspondence to certain depths, and their vertical distribution coincides to some extent with that of their hosts which is well exemplified by specific parasites in Alepocephalidae and Macruridae. Their adaptation to the environmental changes they are exposed to during vertical migrations of their hosts is indicative of ancientness of parasitic fauna formation at great depths. This is also confirmed by the fact that most of these parasites except Myxidium melanocetum, M. melanostigmum, Steringophorus profundum, Steganoderma abissorum, Lecithophyllum bothriophoron, Capillaria kabatai, show a stringent specificity relatively a narrow circle of hosts within the analysed families.

In this connection it may be supposed that the distribution of deepwater parasites is greatly affected by deep currents. As a rule, the temperature of transported waters differs greatly from ambient temperature. This is also typical of the surveyed areas in the North Atlantic with cold waters from the polar regions brought by deep currents. They limit spreading of parasites the life cycle of which is related to benthic animals and promotes that of myxosporidians, parasitic copepods, some polyzonal species the life cycle of which is connected with pelagic animals, and cold-water forms. For instance, of 26 parasite species found in rock grenadier (Macrourus berglax) from the Canadian and European continental slopes and the Reykjanes Ridge only Auerbachia anomala, Gonocerca crassa, Anisakis simplex l., Capillaria kabatai appeared to be common. All of them are very widely distributed. For any two areas eight species were common of which Myxidium melanostigmum, Scolex pleuronectis l., Hysterothylacium aduncum, Echinorhynchus gadi, Clavella adunca are also widespread. Most of these parasites are Arctic-boreal forms and only M.melanostigmum and A.anomala seem to be of Pacific origin but they do not belong to warm water species as they are typical deepwater species. The ranges of all specific parasites of rock grenadier are limited and are smaller than those of their host which is a typical benthophague and does not perform long migrations thus excluding contact between fishes from different areas and the possibility of transfer of their parasites. The similar situation observed for all the analysed fishes related ecologically to the bottom was produced, to our mind, by the isolating effect of deep currents.

In meso-, bathy- and bathyal-pelagic fishes the ranges of typical deepwater parasites, as a rule, coincide to some extent with those of their hosts. This concerns most of the parasites of roundnose grenadier (Coryphaenoides rupestris) slickheads (Alepocephalidae), Moridae and other fishes and is related both with migrations of fish themselves and of different pelagic animals being intermediate hosts for these parasites.

Among the factors affecting vertical distribution of parasites hydrostatic pressure is rather important. This idea expressed earlier by Yu.I.Polyansky (Polyansky, 1958) is proved indirectly by our data. If we analyse the species composition of parasites in deepwater fishes we shall see that none of the parasites typical of the fishes from shallower areas, except polyzonal species, adapted to great depths. Infestation with polyzonal species most likely occurs during daily vertical migrations of deepwater fishes to the thermocline zone where intermediate hosts of these parasites dwell or while preying on meso- and bathypelagic fishes infested with these parasites. Some deepwater pelagic animals seem to be intermediate hosts of these parasites but this point remains unsettled because of its being poorly studied. Acanthocephalan Echinorhynchus gadi (with Amphipoda as an intermediate host) and parasitic crustacean Clavella adunca seem to be the only species adapted to great depths. This is confirmed, in particular, by a high infestation (46.6%) of rock grenadier from the 1200-1300m depths on the Flemish Cap with these parasites. This typical representative of ancient deepwater fishes, leading a settled life, has a low probability of being infested with these parasites at shallower depths.

Many typical deepwater parasites have a wide vertical distribution, which is undoubtedly related with the adaptation of these parasites to vertical migrations of their hosts, both intermediate (plankton vertical migrations have a notable amplitude (Vinogradova, 1959) and definitive. In this case we have a good example of the life cycles of parasites adapting to the peculiarities of their hosts' lives as well as to significant variations in pressure and temperature.

We have already mentioned the few authors dealing with the parasitic fauna of deepwater species who spoke of its getting much poorer with depth both in quality and quantity.

Really, as for freely dwelling organisms, the number of species and their biomass rapidly decline with depth (Zenkevich et al., 1955; Zenkevich, Birshtein, 1955). However, there are some exceptions. In particular, at mean oceanic depths (from 500 to 1500-2000 m) no clear decline in macroplankton quantity, in contrast to mesoplankton, is observed (Brodsky, 1952; Birshtein, Vinogradov, 1955; Vinogradov, 1977). Besides, the ratio of ancient and secondary deepwater organisms changes with depth. For most of secondary deepwater organisms the number of species declines regularly and sharply while that of ancient deepwater animals increases with depth, and only having approached the lower abyssal and ultra-abyssal it starts decreasing (Vinogradova, 1958; Zenkevich, Birshtein, 1961). All this cannot be neglected while studying the formation of deepwater fish parasitic fauna.

Secondary deepwater parasites include all polyzonal species as well as Ortholinea divergens, Ceratomyxa drepanopsettae, C. ramosa, Leptotheca simplex, Steringophorus furciger, Steringotrema ovacutum, Steganoderma formosum, Lepidapedon elongatum, L. rachion, Helicometra plovmornini, Podocotyle reflexa, Stenakron vetustum, S. quinquelobata, Genolinea laticauda, Gonocerca crassa, G. phycidis, Cucullanus heterochrous, Ascarophis arctica, Capillaria kabatai, Lepeophteirus hippoglossi, Hatschekia hippoglossi. Each of these parasites has closely related shallow water species thus proving its consanguinity with shallowwaters. They have not yet managed to isolate morphologically. It is possible that representatives of the genus Schulmania close to Myxoproteus gen. but larger, with thicker shell valves and keel-shaped formations for soaring, belong to secondary deepwater forms. Nearly all the above parasites cannot penetrate below 600-800 m even in ancient deepwater fishes dwelling within a wide depth range. For instance, in rock grenadier and Nezumia bairdi from the 400-600 m depths Genolinea laticuda were found rather frequently (respectively, in 53.3 and 28.6% of the fish analysed). At 900 to 1300 m this parasite disappears. The similar situation is observed with the infestation by Gonocerca crassa and other parasites. Nematoda Capillaria kabatai does not disappear with depth but its occurrence, for example, in Nezumia bairdi from 400-450 and 1100 m depths decreases from 42.9% to 25.0% (mean degree of infestation declines from 1.4 ind. to 1.2 ind. per host). The incidence of infestation by Lepidapedon elongatum, rather significant in fish from 600-700 m depth (31.3% for cod Gadus morhua, the mean degree of infestation being 11.75 ind. per host), decreases noticeably with depth (29.1% and 0.85 ind./host for Trachyrhynch trachyrhynchus , 20.0% and 0.2 ind./host for Lepidion eques, 16.7% and 0.2 spec./host for Coryphaenoides longifilis, 6.6% and 0.13 ind./host for Antimora rostrata). Below 1100 m depth this parasite is not found. Qualitative and quantitative composition of secondary deepwater parasites in such fishes as Licodes esmarki, Glyptorelated shallow water species thus proving its consanguinity with shallow waters. They have not yet managed to isolate morphologically. It is possible that representatives of the genus Schulmania close to Myxoproteus gen. but larger, with thicker shell valves and keel-shaped formations for soaring, belong to secondary deepwater forms. Nearly all the above parasites cannot penetrate below 600-800 m even in ancient deepwater fishes dwelling within a wide depth range. For instance, in rock grenadier and Nezumia bairdi from the 400-600m depths Genolinea laticauda were found rather frequently (respectively, in 53.3 and 28.6% of the fish analysed). At 900 to 1300 m this parasite disappears. The similar situation is observed with the infestation by Gonocerca crassa and other parasites. Nematoda Capillaria kabatai does not disappear with depth but its occurrence, for example, in Nezumia bairdi from 400-450 and 1100 m depths decreases from 42.9% to 25.0% (mean degree of infestation declines from 1.4 ind. to 1.2 ind. per host). The incidence of infestation by Lepidapedon elongatum, rather significant in fish from 600-700 m depth (31.3% for cod Gadus morhua, the mean degree of infestation being 11.75 ind. per host), decreases noticeably with depth (29.1% and 0.85 ind./host for Trachyrhynchus trachyrhynchus, 20.0% and 0.2 ind./host for Lepidion eques, 16.7% and 0.2 spec./host for Coryphaenoides longifilis, 6.6% and 0.13 ind./host for Antimora rostrata). Below 1100 m depth this parasite is not found. Qualitative and quantitative composition of secondary deepwater parasites in such fishes as Licodes esmarki, Glyptocephalus cynoglossus, Hippoglossus hippoglossus, Reinhardtius hippoglossoides decreases with depth. The infestations with polyzonal species both of secondary and ancient deepwater fishes also reduce.

Thus, parasitic fauna of some fishes gets poorer with depth at the expense of secondary deepwater forms and polyzonal species. Manter (Manter, 1934) who dealt with such forms of parasites, indicated scantiness of digenean fauna growing with depth at the coast of Florida.

Slightly different situation is observed in the distribution of ancient deepwater parasites to which belong Myxidium melanocetum, M.melanostigmum, M. profundum, Myxidium sp., Zschokkella kudoi, Sinuolinea magna, Davisia newfoundlandia, Ceratomyxa tenuispora, Leptotheca coelorhyncha, L. quadritaenia, Auerbachia anomala, Palliatus indecorus, Alataspora sp.I., Myxobolus lairdi, Trilospora minuta, Calicotyle affinis, Chimaericola leptogaster, Syncoelicotyle poliorchis, Diclidophora attenuata, D. caudata, D. macruri, D. nezumia, Paracyclocotyle cherbonnieri, Choricotyle oregonensis, Cyclocotyloides pinguis, Atlanticotyle notacanthi, Gyrocotyle fimbriata, Probothriocephalus muelleri, Parabothriocephalus macruri, Philobythoides stunkardi, Gymnorhynchus horridus, Paraccacladium jamiesoni, Antorchis spinosus, Antorchis sp., Antorchis sp. I, Steringophorus pritchardae, S. thulini, Olssonium turneri, Hudsonia agassizi, Zoogonidae gen. sp., Lepidapedon luteum, Bathycreadium elongata, Bathycreadium flexicolis, Bathycreadium Gonocerca macrouri, Dinosoma triangulata, Lecithophyllum anteroporum, Euzetacanthus simplex, Sarcotaces komaii, Chondracanthodes radiatus, Lateracanthus quadripedis, Lophoura bouvieri, Periplexis lobodes, Clavellomimus macruri.

As for the parasitic fauna of separate deepwater species, the number of parasites and degree of infestation decline with depth notably. In Trachyrhynchus trachyrhynchus from the Northeast Atlantic 25 species of parasites were found at the 800-900 m depths and in the central areas only 4 species at the 1500 - 1960 m depths. In rock grenadier from the Northwest Atlantic 8 parasite species were found at the 1200-1300 m depths and 20 species - at the 400-600 m depths. At the same time the parasitic fauna of Nezumia bairdi comprised 8 species at the 1100 - 1130 m depths and 5 species at the 400-450 m depths (Zubchenko, 1981). In Alepocephalus bairdi from the Northeast (1300-1330 m deep), central (1900-1980 m deep) and Northwest Atlantic (500-700 m deep) 12, 11 and 13 parasite species, respectively, were found (Zubchenko, 1984). No significant qualitative or quantitative differences in the parasitic fauna of roundnose grenadier from the 700 to 1600 m depths off the Outer Bailey's Bank were observed (Table 1). Samples were taken every 100 m during 24 hours.

Where does the reason for these discrepancies lie? The analysis of parasitic fauna in Trachyrhynchus trachyrhynchus and rock grenadier showed that among the parasites found in them secondary deepwater (Hepatoxylon trichiuri, Steringophorus profundum, Steganoderma abyssorum, Lepidapedon elongatum, L. rachion, Genolinea laticauda, Gonocerca crassa, Capillaria kabatai, Spinitectus cristatus, Sphyrion lumpi) and polyzonal species (Grillotia erinaceus l., Scolex pleuronectis l., Hemiurus levinseni, Derogenes varicus, Anisakis simplex l., Echinorhynchus gadi) were dominating. Parasitic fauna of the analysed fishes gets poorer primarily owing to the disappearance of these species. At the same time in Alepocephalus bairdi and roundnose grenadier ancient deepwater species such as Myxidium melanocetum, M. melanostigmum, M. profundum, Auerbachia anomala, Palliatus indecorus, Diclidophora macruri, Paraciclocotyle cherbonnieri, Probothriocephalus muelleri, Philobythoides stunkardi, Paraccacladium jamiesoni, Steringophorus pritchardae, Olssonium turneri, Hudsonia agassizi, Gonocerca macrouri, Dinosoma triangulata, Lecithophyllum anteroporum, Lateracanthus quadripedis, Pariplexis lobodes dominate and their number does not decline with depth, though their abundances go down noticeably which may be well exemplified by some parasite species in Alepocephalus bairdi. In the Northwest, Northeast and central Atlantic with comparatively similar incidence of infestation by Steringophorus pritchardae (75.0, 66.6 and 53.3%, respectively) and Hudsonia agassizi (93.8, 62.7 and 60.0%) the mean degree of infestation by these trematodes sharply declines with depth (11.63, 2.33 and 4.1 ind. per host for S. pritchardae and 15.19, 1.98 and 3.73 ind. per host for H. agassizi).

In the first instance scantiness of parasitic fauna in Trachyrhynchus trachyrhynchus and rock grenadier increases with depth at the expense of secondary deepwater species related in their development with benthos and mesoplankton;

in the second case (Alepocephalus bairdi and roundnose grenadier) the qualitative diversity (naturally, relative) is observed at all depths in the fauna of ancient deepwater parasites, the majority of which is related with macroplankton. This is typical of all deepwater fishes and depends on the closeness of relationship between them and the bottom and water mass, on food spectrum (qualitative composition of parasites) and biomass of organisms being intermediate hosts (incidence of infestation).

Thus, secondary deepwater species dominated at great depths, namely, at the depths from 300-400 to 2200 m at the upper bathyal while ancient deepwater parasites - at the lower.

What is the percentage of parasites found in fish from the off-shore areas of the North Atlantic? For ancient deepwater forms Myxosporidia amount to 44.1% of the total amount of these parasites, Monogenoidea - 44.0%, Gyrocotylidae - 100%, Cestoda - 17.3%, Trematoda - 23.6%, Acanthocephala - 20.0%, Crustacea - 16.2%, for secondary deepwater forms Myxosporidia - 23.5%, Monogenoidea - 16.0%, Cestoda - 10.3%, Trematoda - 20.8%, Nematoda - 28.5%, Crustacea - 13.4%. The above figures show that at great depths the most abundant are Myxosporidia and Monogenea, apparently, owing to the direct life cycle in the parasites from these taxons, not complicated by the change of intermediate hosts. Besides, Myxosporidia have developed a number of morphological formations promoting their penetration to great depths. Adaptation to great hydrostatic pressure may be exemplified by Myxosporidia of the genus Myxidium (M. melanocetum, M. melanostigmum, M. profundum) having large spores, thick shell valves, capsules of different size which direct the spore vertically, coarse polar filaments. Myxosporidians of the genus Palliatus and Leptotheca quadritaenia having large spores and polar capsules and, at the same time, mantle-shaped formations and band-like offshoots used for soaring, adapted to parasitizing in bathyal-pelagic fishes. Generally, large spores and polar capsules are typical of deepwater fishes. For instance, Myxidium gigantissimum with gigantic spores more than 100 $\mu$m in size was found in Alepocephalus australis (Dubina, Isakov, 1976).

In other deepwater parasites including those with the complicated life cycle it is difficult to detect any morphological formations. They are probably available in larval freely dwelling settling stages which at certain periods of the life cycle are not protected from the exposure to the environment. In parasites with the complicated life cycle adaptation to a sharp decline in number of species and biomass of intermediate hosts with depth is possibly manifested in high productivity. In particular, representatives of Fellodistomidae, Zoogonidae, Derogenidae, Hemiuridae, being of high fecundity, are the most frequent among trematodes in deepwater fish.

Not all large taxons of parasites are represented at great depths. No leeches were found in deepwater fish and it is hard to say if there are any at all or they may quit their hosts during fish ascending. None of Cilicata and Polyonchinea were found which may be accounted for by recent secondary trasition of the parasites from these groups to other marine fishes. Besides, no representatives of Diphyllidea and Tetraphyllidea or other smaller taxons were observed in deepwater fish.

We consider it interesting that in deepwater fishes large taxons on the level of orders and families relate to ancient and secondary deepwater groups (Andriyashev, 1953; Rass, 1959). The taxonomic rank of the known systematic groups of typical deepwater parasites is an order lower. Thus, at present the following families may be related to them such as Alatasporidae, Trilosporidae, Chimaericolidae, Parabothriocephalidae, Philobythidae of the genera Alataspora, Palliatus, Syncoelicotyle, Paracyclocotyle, Choricotyle, Cyclocotyloides, Atlanticotyle, Hudsonia, Steringophorus, Periplexis, Clavellomimus, and some others not distinguishing, as a rule, by a variety of species. Gyrocotylidae is the only large taxon of parasites typical of large depths.

The peculiarity of deepwater parasitic fauna is mainly manifested at the species level. In this fauna endemic species make up 45.2%, their occurrence being much higher (73.0%) in fishes dwelling at a lower limit of the analysed depths (Coelorhynchus coelorhynchus, C. occa, Coryphaenoides longifilis) compared to such as Alepocephalus bairdi, Trachyrhynchus trachyrhynchus, Coryphaenoides rupestris and Macrourus berglax dwelling within the whole depth range (57.1%). Thus, endemism at the species level grows with depth.

Endemism in higher taxonomic groups is not great, by our data, and is represented by 22 endemic genera of parasites which account for nearly 22.6% of the total number of observed genera, by three endemic families Alatasporidae, Chimaericolidae, Philobythiidae and one class Gyrocotylidea.

It is hard to say if such low endemism at higher taxonomic levels is the consequence of lower rates of evolution of large taxons of deepwater parasites or of comparatively late settling of parasites at great depths. It is possible that the above abiotic and biotic factors affecting the distribution and isolation of species are not the reliable barrier isolating large taxons of parasites. This may also relate to parasites with the direct life cycle including Myxidium melanocetum, M. melanostigmum, Auerbachia anomala, Diclidophora caudata, D. macruri, Cyclocotyloides pinguis, Lateracanthus quadripedis, Periplexis lobodes and others, and some of them (M. melanocetum, M. melanostigmum, A. anomala, C. pinguis, L. quadripedis) are found in the Pacific and Indian Oceans.

Dwelling of parasites with the complicated life cycle in different hosts seems to be a rather good isolation from the environment of the 1st order. This generates high rates of species formation in some groups of parasites which is testified by a high number of species with stringent specificity (61.1%) and the variety of ancient deepwater trematodes increasing with depth.

The role of species with a wide vertical range forming the part of parasitocenoses of deepwater fishes is not great.

All these parasites (Zschokkella hildae, Scolex pleuronectis l., Hemiurus levinseni, Derogenes varicus, Anisakis simplex l., Hysterothylacium aduncum and some others) are also widely spread horizontally. These species do not characterize the ancientness of deepwater parasitic fauna and are late settlers. Namely these species determine on the main the degree of similarity of parasitic fauna in separate deep dwellers.

Thus, the formation of parasitic fauna in deepwater fishes is influenced by a number of factors which are of low importance at shallower depths. This fauna is very specific and comprises a great number of endemic species, and only a small group of world-wide distributed parasites links the parasitic fauna of deepwater fishes with that of shelf and epipelagial dwellers.

For deepwater fish qualitative and quantitative scantiness of parasitic fauna growing with depth at the expense of secondary deepwater forms of parasites is typical. These forms are replaced by ancient deepwater parasites at great depths the qualitative composition of which does not suffer any notable changes at the 400-2000 m depths but the incidence of fish infestation with them declines sharply with depth.

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Table 1. Parasite fauna of roundnose grenadier from different depths of the Northeast Atlantic

| Nos. | Species | 700–800 m | | 800–900 m | | 900–1000 m | | 1000–1100 m | | 1100–1200 m | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Incidence of infestation | Mean degree of infest. | Incidence of infestation | Mean degree of infest. | Incid. of infest. | Mean degree of inf. | Incid. of infest. | Mean degree of infest. | Incidence of infestation | Mean degree of infest. |
| 1. | Myxidium melanocetum | 13.3 | + | 6.6 | + | 13.3 | + | 46.6 | + | 26.6 | + |
| 2. | Myxidium melanostigmum | 40.0 | + | 40.0 | + | 20.0 | + | 60.0 | + | 26.6 | + |
| 3. | Myxidium profundum | – | – | – | – | – | – | – | – | 6.6 | + |
| 4. | Auerbachia anomala | 60.0 | + | 80.0 | + | 80.0 | + | 40.0 | + | 20.0 | + |
| 5. | Declidophora macruri | 26.6 | 0.40 | 33.3 | 1.53 | 40.0 | 1.79 | 26.6 | 0.60 | 60.0 | 1.53 |
| 6. | Parabothriocephalus macruri | 6.6 | 0.20 | 20.0 | 0.47 | – | – | 13.3 | 0.20 | – | – |
| 7. | Scolex pleuronectis l. | – | – | – | – | – | – | – | – | – | – |
| 8. | Pseudophyllidea gen. sp. | – | – | 6.6 | 0.07 | – | – | – | – | – | – |
| 9. | Aporocotyle simplex | – | – | – | – | – | – | – | – | – | – |
| 10. | Paraccaeladium jamiesoni | 6.6 | 0.13 | 26.6 | 0.53 | 33.3 | 0.60 | 6.6 | 0.13 | 6.6 | 0.07 |
| 11. | Gonocerca macrouri | – | – | 6.6 | 0.07 | – | – | 13.3 | 0.13 | 6.6 | 0.07 |
| 12. | Glomericirrus macrouri | – | – | 6.6 | 0.07 | 26.6 | 0.53 | 6.6 | 0.47 | 20.0 | 0.67 |
| 13. | Anisakis simplex l. | 40.0 | 0.93 | 40.0 | 0.67 | 13.3 | 0.60 | 33.3 | 0.60 | 20.0 | 0.40 |
| 14. | Hysterothylacium aduncum | – | – | – | – | – | – | 6.6 | 0.07 | – | – |
| 15. | Hysterothylacium aduncum l. | 20.0 | 0.20 | 6.6 | 1.40 | 13.3 | 0.20 | – | – | – | – |
| 16. | Jonsonmawsonia sp. | 6.6 | 0.07 | – | – | – | – | 6.6 | 0.07 | 6.6 | 0.07 |
| 17. | Lateracanthus quadripedis | 6.6 | 0.07 | – | – | – | – | 6.6 | 0.07 | – | – |

TABLE 1. (Continued).

| Nos. | Species | 1200–1300 m | | 1300–1400 m | | 1400–1500 m | | 1500–1600 m | |
|---|---|---|---|---|---|---|---|---|---|
| | | Incidence of infestation | Mean degree of infest. | Incidence of infestation | Mean degree of infest. | Incidence of infestation | Mean degree of infest. | Incidence of infestation | Mean degree of infest. |
| 1. | Myxidium melanocetum | 20.0 | + | 26.6 | + | 26.6 | + | 53.3 | + |
| 2. | Myxidium melanostigmum | 40.0 | + | 40.0 | + | 40.0 | + | 60.0 | + |
| 3. | Myxidium profundum | 6.6 | + | 6.6 | + | 13.3 | + | 6.6 | + |
| 4. | Auerbachia anomala | 33.3 | + | 53.3 | + | 6.6 | + | 40.0 | + |
| 5. | Declidophora macruri | 13.3 | 0.13 | 20.0 | 0.20 | 13.3 | 0.13 | 6.6 | 0.53 |
| 6. | Parabothriocephalus macruri | – | – | – | – | – | – | 26.6 | 0.27 |
| 7. | Scolex pleuronectis l. | 6.6 | 0.07 | – | – | – | – | 6.6 | 0.20 |
| 8. | Pseudophyllidea gen.sp. | – | – | – | – | – | – | 6.6 | 0.07 |
| 9. | Aporocotyle simplex | 6.6 | 0.07 | – | – | – | – | 13.3 | 0.13 |
| 10. | Paraccaeladium jamiesoni | 6.6 | 0.07 | 13.3 | 0.13 | – | – | – | – |
| 11. | Gonocerca macrouri | 6.6 | 0.07 | – | – | 6.6 | 0.07 | 20.0 | 0.47 |
| 12. | Glomericirrus macrouri | 13.3 | 0.13 | 13.3 | 0.13 | 20.0 | 0.33 | 26.6 | 0.40 |
| 13. | Anisakis simplex l. | 13.3 | 0.13 | 26.6 | 0.27 | 13.3 | 0.13 | 6.6 | 0.07 |
| 14. | Hysterothylacium aduncum | 6.6 | 0.07 | – | – | 6.6 | 0.07 | – | – |
| 15. | Hysterothylacium aduncum l. | – | – | 6.6 | 0.07 | – | – | – | – |
| 16. | Jonsonmawsonia sp. | – | – | – | – | – | – | 13.3 | 0.13 |
| 17. | Lateracanthus quadripedis | – | – | – | – | – | – | – | – |