

## DEEP WATER PARASITES

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### SUMMARY

Few geographically local comprehensive studies on deep-sea parasites have been done. A recent study of parasitism in midwater fishes conflicts with broad generalizations previously advanced. Surveys of demersal fishes and macrofaunal invertebrates in the North Atlantic indicate 1) there is little evidence of coherence and continuity of faunal zones around the ocean basin and 2) that

the community concept should be abandoned because faunal assemblages only persist on a local scale. Parasitological evidence supports this view. The implications are that the parasite species distributions and character of parasite faunas will vary according to the distribution of the fishes and local faunal assemblages.

### RÉSUMÉ : Parasites des eaux profondes.

On possède peu d'étude d'ensemble et géographiquement localisée des parasites dans les mers profondes. Une étude récente sur le parasitisme des poissons de moyenne profondeur est en désaccord avec les généralisations antérieurement proposées. Dans l'Atlantique Nord, les revues des poissons demersaux et de la macrofaune des Invertébrés montrent que 1) on possède peu de preuves d'une cohésion et d'une continuité des zones faunistiques dans

le bassin océanique; 2) le concept de communauté doit être abandonné parce que les ensembles faunistiques ne sont valables qu'à une échelle locale. Les preuves apportées par le parasitisme renforcent cette manière de voir. En effet, la distribution des espèces parasites et les caractéristiques de la faune parasitaire varient avec la distribution des poissons et les ensembles faunistiques locaux.

### *Parasitism in pelagic fishes*

The first comprehensive accounts of deep-sea parasitism concerning mesopelagic and bathypelagic fishes were carried out by Collard (1970) followed by several publications by Noble and coworkers (1973). The data included samples from widely separated localities and, in Collard's study, included 1,087 fish of which 944 were myctophids, mostly juveniles that were vertical migrators. Generalization about the nature of deep-sea pelagic fish parasitism came from these works and were, in part, expansions upon observations made by Gusev (1957).

In contrast is the study of Gartner and Zwerner (1989). Gartner examined 668 fish, 519 (12 spp.) mesopelagic and 149 (6 spp.) of bathypelagic fishes, all from the environs of Norfolk Submarine Canyon (mid-Atlantic Bight). The mesopelagic fishes were predominantly adults and only 18 of the 668 fish were vertical migrators. They found that few of Collard's (1970) generalizations held true when compared with their study of mid-water fishes and concluded that the differences in the results may be explained 1) by geographical region, by feeding of the migrators/non-migrators in their respective pelagic zones; 2) ontogenetic changes associated with diet; 3) bottom association of adult mid-water fishes in continental slope areas; and 4) the influence of slope waters on diets in different geographical regions.

From these two studies and surveys on particular parasite

groups of mid-water fishes it can be said that: 1) mesopelagic fishes harbor many larval parasites common to pelagic prey particular to the given geographical region; 2) the parasite fauna is dominated by larval helminths, especially nematodes; 3) lower prevalences of nematode infections are expected in non-vertical migrators in contrast to vertical migrators; 4) adult helminths are rare but species with relatively low host-specificity may occur; 5) monogenea and acanthocephala are rare; 6) bathypelagic fishes have the poorest parasite fauna overall, with fewer species of parasites but may have adults unique to them; 7) there is little evidence supporting seasonality in mesopelagic fishes; 8) the nature of deep-sea parasitism requires detailed study of specific geographical areas, is locally unique due to differences in fauna and mixing action of water; and 9) collections should not be combined and extrapolated into broad generalizations.

### *Deep sea faunal ecology*

Evidence is accumulating from disparate studies that the deep-sea environment is not as constant as it was once thought. Three tacitly accepted assumptions were vertical faunal zonation of the benthos (Carney *et al.*, 1983), presence of widespread biological communities in the deep-ocean, and that deep benthic communities are unaffected by seasonal changes.

Numerous studies on benthic invertebrate communities have shown that there is little evidence or recurring benthic communities except on a very local scale (Rowe *et al.*, 1982) (Sibuet and Segonzac, 1985). Several investigators (Haedrich and Merrett, 1988) (Mauchline and Gordon, 1984) have found little support for continuity in horizontal

zones among demersal fishes, noting coherence of species and assemblages over only short distances in the North Atlantic. They also note that deep demersal fishes are rarely, if ever, strongly associated with another individual fish species. In pelagial waters, evidence indicates that assemblages are quite random (Haedrich and Judkins, 1979) (Grossman *et al.*, 1982) (Simberloff, 1980). These studies indicate that « communities » in the deep sea may be better considered mosaic assemblages absolutely predictable only in a very local sense. The implication being that diversity of the parasite fauna will probably reflect local ecological diversity of hosts/prey at depth.

Faunal boundaries over depth, *i. e.* in the vertical sense, have been noted (Haedrich *et al.*, 1975) (Haedrich *et al.*, 1980) (Merrett, 1987). A hypothesis (Merrett, 1987), based upon seasonal changes in the overlying water and mixing boundaries in the eastern North Atlantic has been advanced as causes for the striking change in abyssal fish faunal assemblages observed over 7 degrees of latitude. Perusal of the literature shows similar observations on the large-scale distribution of demersal fishes in the northeast Pacific (Percy *et al.*, 1982). This hypothesis, combining both physical and biological oceanographic phenomena, for faunal boundaries in demersal deep-sea assemblages deserves further consideration as it is supported by many other studies (Rice *et al.*, 1986) (Gordon and Duncan, 1985) (Haedrich and Merrett, 1988), including those showing that seasonal surface changes affect deep benthic communities more rapidly than is currently appreciated.

These observations on free-living faunal distribution are probable answers to the disparity in recent findings on parasitism in mesopelagic and bathypelagic hosts and in the absolute nature of the parasite faunas of demersal fishes from different regions. Recent revelations of the distribution of demersal fishes by depth and centers of abundance around the North Atlantic basin further support the observations of Manter (1934) of the similarities of digenetic trematodes in the deep water of Tortugas, Florida having greater trans-Atlantic similarities than to nearby continental shelf waters. Apparently consistent trends in host/parasite « communities » have been noted in vertical and horizontal distribution, mostly for shallow-living fishes and appeared to be true in a general sense for deep-sea fishes as well. However, host/parasite assemblages can differ in an absolute sense over relatively short distances, an observation to ponder in view of recent studies of demersal fish and invertebrate faunal studies in deep waters of the North Atlantic.

The observations of Zubchenko (1981) on contrasts in the parasite faunas of macrourids taken in the Davis Strait, South Labrador area and Flemish Cap agree with our own database in the western North Atlantic (Houston and Haedrich, 1986; Snelgrove, 1980; Campbell and Haedrich, unpublished). The data shows distinct differences in fish and parasite composition and prevalence in different areas.

### *Parasitism in demersal fishes*

Manter's study (1934) of bottom fishes at Tortugas, Florida set the stage for other deep-water studies on demersal fishes. In studying the digenes he found: 1) depth influenced not only free-living populations but also their parasites; 2) no attenuation of trematode fauna with depth (to 1,064 m); 3) prevalence of infection was comparable to shallow-water; 4) of 49 species of trematodes found only two shallow-water species occurred below 100 fathoms; 5) more species of trematodes were common to northern cold waters than to nearby warm, surface waters, suggesting the importance of temperature in the distribution of marine fish trematodes and noted that it might be found that trematodes were distributed from pole to pole in deep-water hosts; and 6) noted the composition of the deep-water trematode fauna was more like the surface fauna of Maine, Great Britain or Norway than nearby shallow-waters at Tortugas. Similarly Armstrong (1974) found a diverse trematode fauna in 21 species of macrourids from the Gulf of Mexico and Caribbean with closer affinities to distant localities. Few large scale, geographically localized surveys have been published dealing with more than one parasite group based upon large sample sizes of the true deep-sea fish fauna that would allow comparisons (Campbell *et al.*, 1980) (Campbell, 1983) (Armstrong, 1974) (Manter, 1934). However, a number of authors, Zubchenko and Rohde in particular, have contributed and provided insight into ecological trends in parasite distribution among marine fish populations (Rohde, 1978, 1985, 1986, 1988) (Zubchenko, 1980, 1981, 1985) (Scott, 1987). The life-history studies of Koie (1985) are particularly important in this regard. A recently completed study by Heath (1989) will provide the first detailed study in the southern hemisphere.

Campbell and his colleagues (1980) studied 1,763 specimens of demersal fishes (22 families, 37 genera, 52 species) in the New York Bight. 1,556 of the fishes were taken from depths of 200-5,000 m. Of the deep-living teleosts examined 9 species were macrourids (905 fish) and 37 species (850 fish) were non-macrourid teleosts. Overall prevalence of metazoan parasites was 87. % for macrourids and 71.4 % for the remainder. Eighty percent of all fishes examined were infected with 1-12 ( $x = 2.6$ ) species of parasites. More than 17,000 helminth parasites (80 spp.) and 137 copepods (10 species; 7 below 200 m) were found from the 52 species of fishes. Nematodes showed higher prevalence, but digenes were more abundant. Cestodes, acanthocephalans and copepods followed in decreasing order of prevalence. Macrourid hosts showed high prevalences and mean intensities of infection, but non-macrourid teleosts carried the bulk of the parasites recovered. This study was compared to other deep-sea collections from elasmobranchs and pelagic species and to other studies in a later publication (Campbell, 1983).

For the assemblage of deep-benthic fishes along the continental margin of the New York Bight, Campbell *et al.* (1980, 1983) found the following:

1. Mean parasite loads in deep-living benthic fishes are directly related to fish population densities.

2. More species of metazoan parasites occur when fish population densities are higher, agreeing with the theoretical relationship between host population density and number of macroparasites per host.

3. Infection of the slope dwelling rattail, *Coryphaenoides armatus*, decreases in number of species and intensity as depth increases. The decrease accompanies the decrease in macrofaunal abundance with depth.

4. Three ontogenetic patterns of parasite recruitment could be recognized; exemplified by *C. armatus*, by *C. carapinus*, and by *Nezumia bairdii* and *Alepocephalus agassizi*.

5. Host-specificity of monogenea and digena were high.

6. Similarity indices of parasite faunas reflected overlaps in diets of co-occurring species agreeing with dietary studies showing varying degrees of selectivity by generalized feeders, and the presence of specialized feeders in the deep sea.

7. The parasite fauna of *C. armatus* changed directly with consumption of certain prey.

8. The continental rise dwelling rattails *Nezumia bairdii* and *Coryphaenoides armatus* living in the canyon were more frequently and more heavily infected than those living on the adjacent slope at depth.

9. The deep-water parasite fauna was less diverse compared to shallow-water faunas; for digenea, fewer genera and species were found compared to Manter at Tortugas, Florida (Manter, 1934) or Armstrong (1974) in the Gulf of Mexico.

10. Host-specificity for both monogenea and digena was high and was closely similar to the findings of Armstrong (1974) and Manter (1934). Monogenea showed oioxenic specificity; most digenes and cestodes were oioxenic or stenoxenic, and acanthocephalans and nematodes were euryxenic in our samples.

11. Parasitism in these fishes appears independent of season.

Except for the widely occurring species of larval nematodes, most of the parasite species found were confined to deep-water hosts. Of the deep-water species, several are known to be more widely distributed to the north, several others have trans-Atlantic distributions in the same or related hosts in the NE Atlantic. Recent host records from other geographical areas indicate a lesser host-specificity status for some species.

#### *The continental margin effect*

Until very recently, the assumption has been that at a given depth that conditions and faunas are similar across the oceans at that depth. Campbell (1983) raised this question about the distribution of the parasite fauna away from the continental margin. A summary of nine deep-sea trawling surveys in the North Atlantic basin has been presented (Haedrich and Merrett, 1988) which shows that 5 families dominate the deep demersal fish fauna at slope (< 750 m), rise and abyssal depths (> 4,500 m) and the distributions

of the fish species were typically discontinuous without repeatable patterns of distribution by depth on the slope or rise and that depths of relative abundance vary considerably. Furthermore, Haedrich and Merrett (1990) examined the concepts of continuity and community and found that indices of similarity and overlap are low indicating that both assemblages and fish species retain coherence over only short distances. Only two fish species of 325 collected were widespread and abundant. The significance of these works is to show that there is little evidence for faunal zonation or communities in the deep sea. Furthermore, the trans-Atlantic and latitudinal contrasts in diversity and distribution are reflected in studies of the invertebrate fauna (Haedrich and Maunder, 1984). Transitions in these free-living assemblages should affect the composition of the parasite faunas as well.

#### *Zoogeography*

The picture is far from complete. Reports from surveys are too numerous to list here but new taxa and host records are revealing a far-ranging distribution for many genera and species particularly within the distribution of genera and families of hosts (Bray, 1987) (Bray and Gibson, 1988). Host records in the literature indicate the presence of several parasite faunas. They are:

- 1) a « true » deep-sea fauna limited to deep-sea hosts;
- 2) parasite species that have invaded from shallow-water environments; and
- 3) cosmopolitan species occurring in a wide range of hosts at shallower depths.

True deep-sea parasite faunas tend to show little or no relationship to nearby shallow faunas, instead having close affinities to deep-sea faunas of distant geographical regions. Some species have been reported at shallower depths at high latitudes. A bipolar distribution is known for some genera in the Atlantic and Pacific or distribution above high latitudes of the same ocean is known for others. The degree of parasite species endemism among oceans appears high but within the ocean basins themselves is not generally well-known with distance from the continental margins onto the abyssal plain. Predictably, in the North Atlantic, parasite endemism will parallel that of the fishes on the continental slope where endemism is highest (Haedrich and Merrett, 1988).

Comparison of parasite faunas of fish in the North Atlantic with the distribution of fish species indicates that it may be oceanographic characteristics instead of physical proximity that provide the underlying causal explanation for the similarities and distinctive nature of the parasite fauna by depth and over distance. Aspects of both physical and biological oceanography affect the community composition and prey available to fishes. The physical environment affects small organisms (like pelagic forms) more than larger ones. Current circulations are likely very important in distribution patterns of parasites and free-living organisms by affecting continental slope communities and trans-oceanic distributions. In pelagic waters it is rather well estab-

blished that water of different temperatures characterise different assemblages of organisms. Arguments in support of this are: 1) one finds the same species of animals within closed circulation systems or connected areas rather than those that are not; 2) the diversity of prey available is greatest in areas of mixing rather than in uniform water mass-similar to an ecotone effect on land; 3) parasite success is dependent upon population density; and 4) the mechanism for temporal change in species abundance involves biotic and abiotic factors.

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