Why do fish have so few roundworm (nematode) parasites?*

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Synopsis

Although they are the oldest and most diverse members of the subphylum, the fishes have relatively few nematode parasites in comparison with other vertebrate classes. It is hypothesized that this paucity of parasite species has occurred because nematode parasites first evolved in terrestrial hosts and only a few lines of these parasites were able to transfer to fish after the appearance of heteroxeny (use of intermediate hosts) and paratenesis (use of transport hosts). The inability of nematodes to initiate parasitism in aquatic ecosystems restricted fish parasites mainly to forms first adapted to terrestrial vertebrates and at the same time deprived large groups of aquatic invertebrates such as the crustaceans, annelids and molluscs of a nematode parasite fauna.

Of the approximately 2280 known genera of nematodes, about 33% (766) occur as parasites of vertebrates but of these only about 11% (88) occur in fishes, a puzzlingly low number for a vertebrate group consisting of some 25000 recent species (over 50% of recent vertebrates). According to an early compilation (Yamaguti 1961) only about 12% of the nematode species known from vertebrates occur in fishes, thus the relative number of genera in fish also apparently reflects the relative number of species.

An up-to-date enumeration of all the species of nematodes reported in fishes has not been undertaken but regional lists readily reflect their relative paucity. For example, Hoffman (1967) listed only 58 species in all the freshwater fishes in North America. Also, Margolis & Arthur (1979) listed 50 species in the marine and freshwater fishes in Canada, whereas Wong et al (1990) listed 162 species in birds in Canada. Most recently, Moravec (1994) compiled

information on the 58 nematode species described from freshwater fishes in Europe. This number contrasts with the some 100 species reported in amphibians and reptiles in Europe where the diversity of these vertebrates is comparatively limited; worldwide about 1170 species of nematodes are known from amphibians and reptiles, most in warmer parts of the world where these animals flourish (Baker 1987). It would be a laborious and probably unrewarding task to attempt to enumerate the numbers of nematode species described from birds and mammals but it is probably in the range of 4–5000 species (one superfamily, the Trichostrongyloidea has some 1050 species!). How, therefore, do we account for the fact that nematodes have been so relatively unsuccessful in invading the parasitic environment provided by fishes, the most speciose and most ancient group of vertebrates and the progenitors of the higher vertebrates?

The answer seems to lie in the origins of parasitism among the nematodes. The Phylum Nematoda
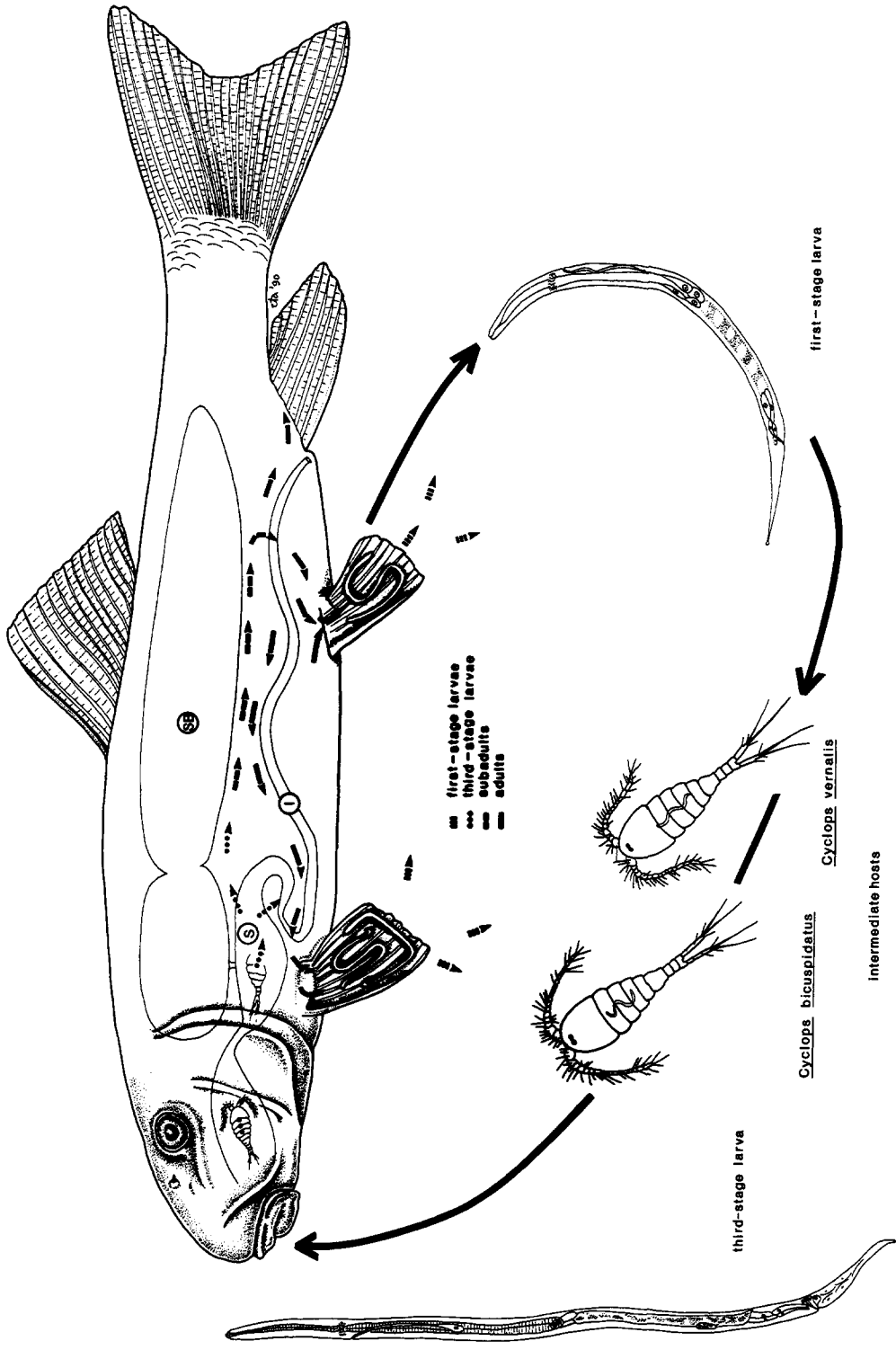
Fig. 1. A typical heteroxenous life cycle of a nematode in fish, the development and transmission of *Philometroides huronensis* of white suckers, *Catostomus commersoni,* in Lake Huron, Ontario. Gravid female worms in fins release first-stage larvae which enter the water. First-stage larvae are predated by copepods in which they develop to the infective stage. Fish acquire infections by ingesting copepods containing infective (third-stage) larvae. Larvae migrate to the region surrounding the swim bladder and develop to small adults. Females are inseminated and males die. Females eventually migrate to the fins, become gravid and release larvae through a break in the skin (after Anderson 1992).

is divided into two classes, the Adenophorea and the Secernentea. The former includes the numerous marine nematodes and a few freshwater and soil nematodes, including a predacious group, the dorylaimids. The Secernentea embraces the vast majority of soil-dwelling nematodes including the ubiquitous rhabditids, which are bacterial feeders, and the tylenchids and aphelenchids which feed on plant cells and fungi.

It is striking that 98% of all genera found in vertebrates belong to the Secernentea and that they can be traced back to the soil-dwelling, bacteria-feeding nematodes of the family Rhabditidae. In addition, the few genera found in vertebrates which belong to the class Adenophorea seem clearly to have been derived from soil-dwelling dorylaimids with their characteristic stylet (Steiner 1917). There is, therefore, no evidence that any aquatic nematodes ever successfully evolved towards parasitism even though these organisms undoubtedly have shared marine and freshwater ecosystems with fishes for millions of years. We conclude, therefore, that parasitism in nematodes must have originated on land and not during that prolonged period when fishes were the only vertebrates on earth (Anderson 1984, 1988, 1992). This conclusion is at variance with an alternative hypothesis that nematode parasites originated in fishes and were then transferred to land with the origin of the tetrapods (Osche 1963, Inglis 1965).

The hypothesis that nematode parasitism did not originate in aquatic habitats is strongly supported by the fact that nematode parasites are essentially non-existent in aquatic crustaceans, molluscs and annelids (polychaetes and oligochaetes) but are common among their terrestrial counterparts in the insects, terrestrial gastropods and the earthworms. One is forced to conclude that nematodes found in the terrestrial invertebrates originated in soil and not in water.

When the first land vertebrates appeared they undoubtedly encountered the soil-dwelling rhabditids which had developed the dauer larva, a resistant dispersal stage, and it is probably through this remarkable larva that the secernenteans were able to invade the tissues of early terrestrial vertebrates. Dauer larvae, first discovered by Maupas (1899)

and named by Fuchs (1937), are modified early third-stage larvae (there are five stages separated by four moults in the development of all nematodes), and it is significant that in the many secernentean parasites of vertebrates, it is almost always the early third-stage which invades the host. A dauer larva does not occur in aquatic free-living nematodes. Also, nematodes lost kinocilia during the course of their evolution and are therefore ineffectual swimmers in contrast to the free-living ciliated stages of trematodes and cestodes which make these helminths highly successful in aquatic ecosystems. The loss of cilia and the inability to swim effectively could have made contact between nematodes and potential hosts difficult or impossible in aquatic environments and this may have precluded the initiation of parasitism among the free-living marine and freshwater nematodes.

It is necessary, however, to account for the fact that 80–90 genera of nematodes do occur as adults in fish hosts. The vast majority of the nematode parasites of fish use intermediate and paratenic (transport) hosts which enable them to be transferred through the food chain to the fish host in an aquatic environment (Anderson 1992, Fig. 1). In addition, of the 17 families of nematodes occurring in fish, only 5 are unique to fish. Thus 71% of all families of fish nematodes are related to those in terrestrial vertebrates. Also, there is not a single nematode superfamily or order that is unique to fishes. One concludes, therefore, that fish nematodes lack uniqueness and are related to nematodes in terrestrial vertebrates.

The earliest nematode parasites of vertebrates probably had direct life cycles without intermediate hosts (*monoxeny*). The tendency to isolate the free-living stages from the rigours of the external environment (known as '*seclusion*') eventually gave rise to *heteroxeny* or the use of intermediate hosts in which development to the infective stage took place. The evolution of transport hosts (*paratenesis*) probably adapted *heteroxeny* to the changing food habits of the host during the radiation of the vertebrates. With the appearance of heteroxeny and paratenesis in terrestrial vertebrate parasites, opportunities for transfer to the aquatic ecosystem appeared. Two major lines of nematodes trans-
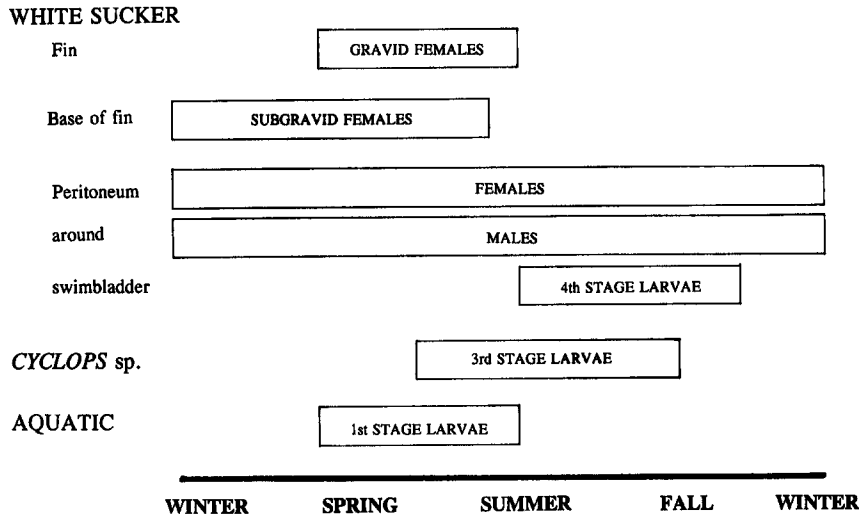
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Fig. 2. The seasonal cycle of *Philometroides huronensis* of the white sucker, *Catostomus commersoni* in Lake Huron Ontario. Females in fins release larvae in spring. Copepod intermediate hosts predate the larvae which invade the haemocoel of the copepods and reach the infective stage. Copepods with infective larvae are ingested by fish in summer and fall. Worms reach the fourth and subadult stages around the swim bladder and females are inseminated by fall. Males die but inseminated females migrate to the base of the fins and remain there until spring when they will move into the fins, become gravid and release their larvae through a break in the skin (after Uhazy 1977).

ferred to fishes, one utilizing arthropods as intermediate hosts and one utilizing prey vertebrates as intermediate hosts. Patterns of transmission of each line adapted to the behavior of fishes. New parasites could not evolve from free-living forms in aquatic habitats. Thus the nematode fauna of fishes is restricted, lacks the diversity found in terrestrial vertebrates, and retains systematic affinities to forms in terrestrial hosts from which they have evolved.

In addition to the heteroxenous groups, a few pinworms (Oxyurida) occur in fishes in subtropical and tropical regions. Oxyurids are the only nematodes found in both vertebrates and invertebrates and it is assumed the forms in vertebrates were derived from those in insects (Chitwood & Chitwood 1950). Eggs of oxyurids are directly infective to the host and presumably these nematodes are restricted to fishes with the necessary behavioural and ecological peculiarities which makes contaminative transmission possible. Pinworms could have invaded fishes prior to the appearance of the tetrapods but they are common in amphibians and reptiles and may have first adapted to land vertebrates before invading fishes.

Although the nematode fauna of fishes is rela-

tively limited, a number of species are significant pathogens and deserve investigation. Also, fishes serve as intermediate or paratenic hosts of several nematode parasites of piscivorous birds and mammals. For example, species such as *Pseudoterranova decipiens* (of seals) and *Anisakis simplex* (of toothed whales) have sizeable larvae in marine fishes which make the flesh unsightly and can pierce the gut of humans if ingested. Fishes and their parasites are also excellent models to study host-parasite relationships and their evolution and epizootiology because they can usually be captured in numbers, aged and sexed with ease. Some species are valuable experimental animals which can be reared parasite-free and in uniform sizes and of known genetic history. There are also fewer ethical restrictions in experimenting with fishes than mammals or birds. Unfortunately, our knowledge of the biology of fish nematodes is limited to about 31 species (cf. 529 species studied, mainly in mammals and birds, often in great detail) (Anderson 1992) and most information is restricted to field data and the determination of intermediate hosts. There is a dearth of experimental studies to elucidate the behaviour of nematodes in the host and the factors involved. To study

behaviour of nematodes in ectotherms like fishes it will probably be necessary to mimic natural conditions experimentally since the life cycles of many fish nematodes are known to be related to the seasons (Fig. 2).

Acknowledgements

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