Vol. 18: 11-20, 1994 | DISEASES OF AQUATIC ORGANISMS Dis. aquat. Org. | Published January 27

Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary

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ABSTRACT: A 1 yr study was conducted to determine which fish species may play a role in the life cycle of *Anguillicola crassus* in various habitats of Lake Balaton, Hungary. The prevalence and intensity of the larval infection of fish species acting as paratenic hosts was studied, and observations were made on the types of paratenic host reactions against larvae. With the exception of 1 species, all 20 fish species were infected by *A. crassus* larvae; however, the prevalence and intensity of infection varied widely. Six species (asp, white bream, Chinese rasbora, pike, river goby, European catfish), hitherto unreported as paratenic hosts, also proved to be infected by larvae in Lake Balaton. Of the 13 fish species examined in large numbers, ruffe and European catfish showed the highest prevalence of infection (100%), followed by river goby (83%), white bream (79%) and bleak (68%). Of these 13 fish species, ruffe showed the highest intensity of infection by live larvae (mean intensity: 39.3 3rd stage larvae, L_3), followed by European catfish (mean number of live larvae: 26.9) and river goby (mean number of live larvae: 9.1). The mean number of live L_3 in bleak, a species regarded as the principal food source for eels, was 4.1. Specimens containing only dead or both dead and live larvae were much more common in cyprinid fishes than in species belonging to other taxonomical entities. In these fish, the process of encapsulation and subsequent necrosis of live larvae could also be observed. With knowledge of the feeding habits of eels, it appears that bleak play the most important role in the transmission of anguillicolosis. Other intensively infected fish species (e.g. ruffe) may also contribute to massive infection of individual eels, even if they have a lower share in the eels' food structure.

KEY WORDS: Eel parasite · *Anguillicola* · Paratenic hosts · Lake Balaton (Hungary)

INTRODUCTION

The parasitic nematode *Anguillicola crassus* (Nematoda: Dracunculoidea) was brought into Europe from Southeast Asia with Japanese eel stocks imported for consumption and further breeding in the 1980s (Peters & Hartmann 1986). It then rapidly spread throughout the European continent from west to east (Neumann 1985, van Banning et al. 1985, Canestri-Trotti 1987, Dekker & van Willigen 1987, Taraschewski et al. 1987, Dupont & Petters 1988, Hellström et al. 1988, Koie 1988, Belpaire et al. 1989, Kennedy & Fitch 1990, Székely et al. 1991, Cruz et al. 1992), probably as a result of insufficiently controlled live fish transportations (Belpaire et al. 1989). The original host of *A. crassus* is the Japanese eel *Anguilla japonica*, in which the infection does not give rise to major lesions (Egusa 1979), while in the European eel *Anguilla anguilla* it may give rise to severe pathological changes (van Banning & Haenen 1989, van Willigen & Dekker 1989, Kamstra 1990, Molnár et al. 1993). Mortality due to anguillicolosis in cultured European eels has been described by Sarti et al. (1985), Hartmann (1987), Liewes & Schaminee-Main (1987), Mellergaard (1988) and Boon et al. (1989). Repeated mortality caused by *A. crassus* in eels living in natural waters has been reported by Molnár et al. (1991, 1993) and Bíró (1992) from Lake Balaton, Hungary.

The life cycle of *Anguillicola crassus* was studied by De Charleroy et al. (1990). Adult *A. crassus* specimens live and reproduce in the swimbladder of eels. The eggs excreted by the female helminths contain 2nd stage hatching or hatched larvae which are consumed by copepods upon their release into the outside world. After moulting in the body cavity of copepods, 3rd stage larvae emerge which are infective to eels. The copepods containing the larvae are either consumed directly by eels which thus become infected, or serve as food source for another fish species, a so-called paratenic host. The 3rd stage larvae do not develop further in the paratenic host, or in exceptional cases develop into 4th stage larvae.

Fish species acting as paratenic host also play a role in the feeding of eels of larger body size. According to Paulovits & Bíró (1987), in the early spring and autumn period the eels of Lake Balaton mainly feed on non-biting midges (Chironomidae) in the pelagic zone, while from May to August their principal food source is constituted by the bleak in the littoral zone.

Infection of paratenic hosts by *Anguillicola crassus* larvae has been reported by only a few researchers. De Charleroy et al. (1990) experimentally infected common carp *Cyprinus carpio* with 3rd stage larvae. *A. crassus* larval infection of paratenic host fish living in natural waters has been studied by Cannaerts (1989), Haenen & van Banning (1990), Thomas & Ollevier (1992) and Höglund & Thomas (1992).

This study, which encompassed a 1 yr period, was aimed at determining which fish species may play a role in the life cycle of *Anguillicola crassus* in different habitats of Lake Balaton, Hungary. The prevalence and intensity of larval infection of paratenic host fish species were studied, and observations were made on the type of anti-larval host reactions occurring in the different paratenic host species.

MATERIAL AND METHODS

Sampling. Between September 1991 and September 1992, fishes belonging to different species, of a size suitable for eel food (not exceeding 14 cm in body length, with the exception of the pike with a mean body length of 24.7 cm) were collected by electrofishery in 7 habitats of Lake Balaton in the stony and reedy parts of the littoral zone. The sampling sites were located in the eastern, central and western areas of the 77 km long and 4 to 8 km wide (minimum 1.5 km, maximum 14 km) lake; thus, the fish caught represented the entire fish population of the littoral region of Lake Balaton.

Characterization of Lake Balaton. This section, which is perhaps a bit more detailed than usual, is needed to understand the unique characteristics of anguillicolosis in Lake Balaton.

As compared to its vast water surface, Lake Balaton is an extremely shallow lake (average water depth: 3.2 m), with deviations in water quality between different regions of the lake. In the summer season, the water temperature may be permanently above 20 °C, with temperatures exceeding 25 °C for some weeks every summer and, in extreme cases, with water temperatures as high as 28 to 31 °C on some days. In winter the lake is covered by a thick layer of ice. Due to the organic matter load discharged into the lake by the river Zala, the biggest stream running into the lake, the western basin of Lake Balaton is of eutrophic character. The central part of the lake shows a steadily improving water quality, while the eastern basin is oligotrophic, due to the deeper water and the good water quality of the small streams running into it.

In connection with the water quality, the quantity of plankton and, thus, of *Anguillicola crassus* intermediate hosts (copepods) is much higher in the western than in the eastern basin. In the littoral region, the dominant copepods are *Eudiaptomus gracilis* and *Cyclops* spp. (Simonian et al. 1993).

The eel population shows uneven distribution in the lake. Probably because of the better food supply, the eel stock of the western basin is bigger. The eel population of Lake Balaton was estimated in 1991 at about 1000 t. Due to the better than expected results of intensive eel fishing started after the eel mortality of 1991, the current eel population of the lake can be put at 1500 to 2000 t. This highly intensive eel stock originates from the 2 to 4 million glass eels regularly introduced into the lake every year except in 1988 to 1990. Regarding the composition of the eel population, in recent years the proportion of larger specimens has increased because of the 3 yr interruption of stocking and the impossibility of transmigration. Transmigration and trapping of eels in the lake's only drain channel (Sió Canal) became impossible as water drainage was suspended during the past dry years. The proportion of older eels will increase within the population because the introduction of eels was prohibited once and for all after the mass eel mortality of 1991 (Molnár et al. 1991).

According to a study of species structure performed by Simonian et al. (1993) between May and October 1991, the fish fauna of Lake Balaton in the littoral region (which is one of the main habitats and feeding areas of the eel) comprises 23 species. Cyprinids represented 92.5% of the 5256 specimens tested: bleak *Alburnus alburnus* 38.7%, bitterling *Rhodeus sericeus amarus* 15.6%, roach *Rutilus rutilus* 15.1%, rudd *Scardinius erythrophthalmus* 12.6%, and bream *Abramis brama* 5.5%. The proportion of percids was 5.8% while that of fish species belonging to other taxonomic groups constituted 1.8%. The fish species composition of benthic areas under the pelagic zone (which are also considered an eel habitat) is probably different; however, no data are available on such areas.

Methods. The small fish caught by electrofishery were transported live to the laboratory in aerated tanks and kept in aquaria until dissected. Due to the effect of season, weather conditions and other factors, the samples collected at the individual sampling times differed in both species composition and specimen number. Thus, many species are included in almost every sample, while others were examined once or on a few occasions only.

The body length of the fish was recorded before dissection. After opening the body cavity, fresh squash preparations were prepared from the entire substance of all inner organs between 2 slides. By examining the preparations in a light microscope, the number of 3rd stage larvae was recorded. Fish specimens not infected by larvae were distinguished from the infected specimens. The infected fish were assigned to one of 3 categories: fish infected only by live larvae, fish infected only by dead larvae, and fish infected by both live and dead larvae.

Squash preparations prepared from fish showing massive infection were microphotographed. Certain heavily infected organs of the fish were fixed in Bouin's solution, sectioned by histological techniques, the sections were stained with haematoxylin and eosin, and microphotographs were taken of them. The host reaction, if any, developing around the larvae was evaluated on the basis of the fresh and histological preparations and the microphotographs.

RESULTS

The 669 fish specimens collected for processing at 7 sampling sites on a total of 15 occasions during the 12 mo period of study belonged to 20 species. The species most represented in the sample was the bleak (n = 176). Thirteen of the fish species were represented by more than 10 specimens in the sample. The results are presented in Table 1 and in Figs. 1, 2 & 3.

Appearance and identification of the larvae

Besides 3rd stage *Anguillicola crassus* larvae, in many cases other helminths (nematodes, trematodes and cestodes) could also be found in the abdominal cavity of the fish examined; however the occurrence of these latter worms was not recorded. With some experience the *A. crassus* larvae were easily distinguishable from other nematodes, first of all by the typical pointed labia located at the worms' anterior end. Infection intensities similar to those found for *A. crassus* were not observed for any other nematode. By their agile motion the live larvae were easily distinguishable from the dead ones. In some cases the encapsulated larvae showed slow motion, while others did not move at all during a long period of observation. In the classification I adopted these larvae were assigned to the category of 'live encapsulated' and 'dead encapsulated' larvae respectively.

Prevalence and intensity

All but one of the fish species included in the study proved to be infected by *Anguillicola* larvae. The prevalence and intensity of infection markedly differed by species. Of the 13 species represented in the sample with at least 10 specimens, ruffe and European catfish showed the highest prevalence of infection (100%), followed by river goby (83%), white bream (79%) and bleak (68%). In the remaining cyprinid species examined in relatively large numbers the prevalence of infection was 36 to 72%. The lowest prevalence of *Anguillicola crassus* infection (6%) was demonstrable in pike perch (Fig. 1).

Of the 13 fish species most represented in the sample, ruffe showed the most intensive infection with live larvae (mean intensity: 39.3 3rd stage larvae). European catfish also had an infection of high intensity, with the mean number of live larvae being 26.9. The third most infected species was river goby (with a mean live larval count of 9.1). In the bleak, the mean number of live 3rd stage larvae was 4.1, while in the other species examined this value was between 1 and 3.7.

Infection by dead *Anguillicola crassus* larvae was by far the most expressed in European catfish (with a mean larval count of 188) and could be considered high in ruffe (25 larvae), rudd (22.9 larvae), asp (21.3 larvae) and roach (18.5 larvae). The bleak specimens contained 13.2 dead larvae on the average, while in the other species the number of dead larvae was lower (8.5) (Fig. 2).

Miscellaneous infections

Of the fish species examined in relatively large numbers, in cyprinids the proportion of specimens containing only dead larvae or both dead and live larvae was much higher than in species belonging to other taxonomical entities. Thus, practically all specimens of pumpkinseed (96%), pike perch (100%), river goby (100%), European catfish (92%) and ruffe (100%) contained live larvae (Fig. 3). Almost all specimens (93%) of certain cyprinid species (e.g. bitterling) contained only dead larvae, but most other cyprinids also showed a high ratio of infection by dead larvae or a combined infection by both dead and live larvae (rudd 97%, white bream 96%, roach 85%, bleak 87%). The cyprinid species showing the lowest ratio of infection

Table 1. *Anguillicola crassus*. Larval infection of paratenic fish host species from Lake Balaton, Hungary. Summary of all fish species examined during the 1 yr period from September 1991 to September 1992. Int.: mean intensity

Fish species	No. examined	Mean length (cm)	No. not infected	No. infected by: Dead larvae only n	Int.	Both live and dead larvae n	Live int.	Dead int.	Live larvae only n	Int.	Prevalence (%)	Summarized int. Live	Dead
Cyprinidae													
Abramis brama (bream)	25	5.8	16	5	3.4	1	5	1	3	2	36	2.75	3
Alburnus alburnus (bleak)	176	7	57	50	17.1	54	4.6	9.5	15	2.5	68	4.1	13.2
Aspius aspius (asp)	6	10.5	1	2	30.5	1	3	3	2	3.5	83	3.3	21.3
Blicca bjoerkna (white bream)	67	7	14	40	8.2	11	2	9.6	2	2.5	79	2.1	8.5
Carassius auratus gibelio (gibel carp)	26	8	12	4	3.3	5	3.4	2.8	5	2.2	54	2.8	3
Gobio gobio (gudgeon)	1	3.7	0	0	0	0	0	0	1	1	100	1	0
Cyprinus carpio (common carp)	3	10.6	1	0	0	2	13	9	0	0	67	6.5	9
Leucaspius delineatus (rain bleak)	1	5.7	1	0	0	0	0	0	0	0	0	0	0
Pseudorasbora parva (Chinese rasbora)	62	5.5	24	15	4.1	7	4.7	6	16	3.3	61	3.7	4.7
Rhodeus sericeus amarus (bitterling)	45	5.1	17	26	5	0	0	0	2	1	62	1	5
Rutilus rutilus (roach)	80	6.7	27	32	23.4	13	2.5	6.5	8	3.5	66	2.9	18.5
Scardinius erythrophthalmus (rudd)	47	7.8	13	20	25.5	13	2.3	18.8	1	1	72	2.2	22.9
Tinca tinca (tench)	4	11.7	2	0	0	1	1	12	1	2	50	1.5	1
Centrarchidae													
Lepomis gibbosus (pumpkinseed)	121	5.8	46	3	2.3	4	2.8	2.8	68	3.1	62	3.1	2.6
Percidae													
Perca fluviatilis (perch)	3	10.9	1	0	0	0	0	0	2	3	67	3	0
Gymnocephalus cernua (ruffe)	17	7.5	0	0	0	16	40.8	25	1	15	100	39.3	25
Stizostedion lucioperca (pike perch)	17	8.3	16	0	0	0	0	0	1	3	6	3	0
Esocidae													
Esox lucius (pike)	8	24.7	7	0	0	0	0	0	1	1	13	1	0
Siluridae													
Silurus glanis (European catfish)	12	13.3	0	1	1	11	29.3	205	0	0	100	26.9	188
Gobiidae													
Neogobius fluviatilis (river goby)	81	7.5	14	0	0	14	9.3	2.4	53	9	83	9.1	2.4

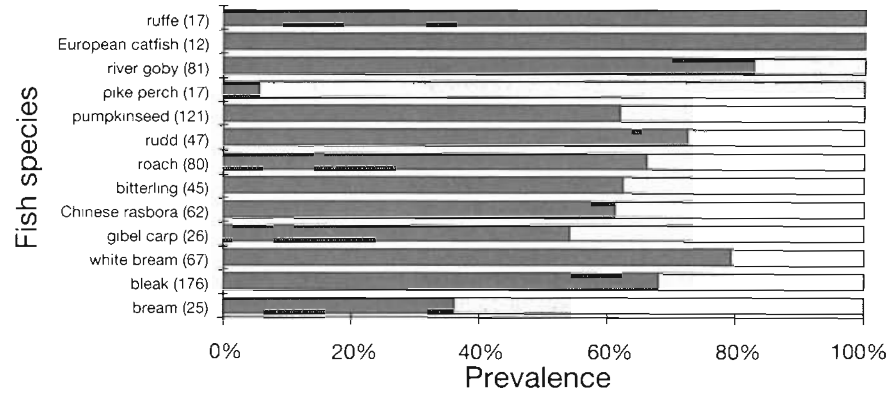


Fig. 1. *Anguillicola crassus*. Prevalence of infection in paratenic hosts sampled (at least 10 specimens). No. of individuals examined is indicated for each species

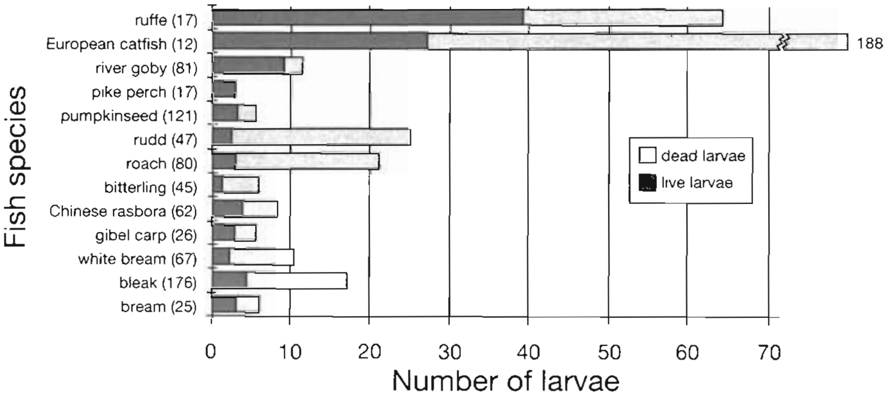


Fig. 2. *Anguillicola crassus*. Mean intensity of infection in paratenic hosts sampled (at least 10 specimens)

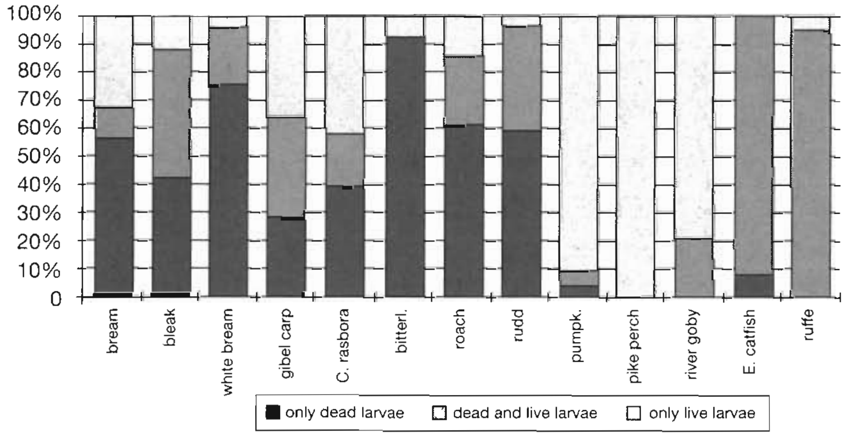


Fig. 3. *Anguillicola crassus*. Comparison between the different types of infection in infected paratenic hosts sampled (at least 10 specimens)

by dead larvae only or by dead plus live larvae included Chinese rasbora (58 %), bream (67 %) and gibel carp (64 %).

Host reaction in the paratenic hosts

In the paratenic hosts, the 3rd stage larvae of *Anguillicola crassus* occurred in the abdominal cavity, in various organs or on the surface thereof. Most larvae could be observed on the outer surface of the intestinal wall or stomach and in the genital organs but some occurred also in the wall of the swimbladder and in the liver. Besides the freely occurring live larvae, in many fish still-living larvae encapsulated by the host organism could also be found (Fig. 4a, b). The capsules formed around the larvae were elongated (Fig. 5a, b) in shape in most cases (primarily in cyprinids and ruffe) and spherical (Fig. 6) at other times (e.g. in European catfish). The structure of encapsulated larvae was still well discernible; however, the larvae no longer showed signs of life (Fig. 7). In many cases, the capsules pre-

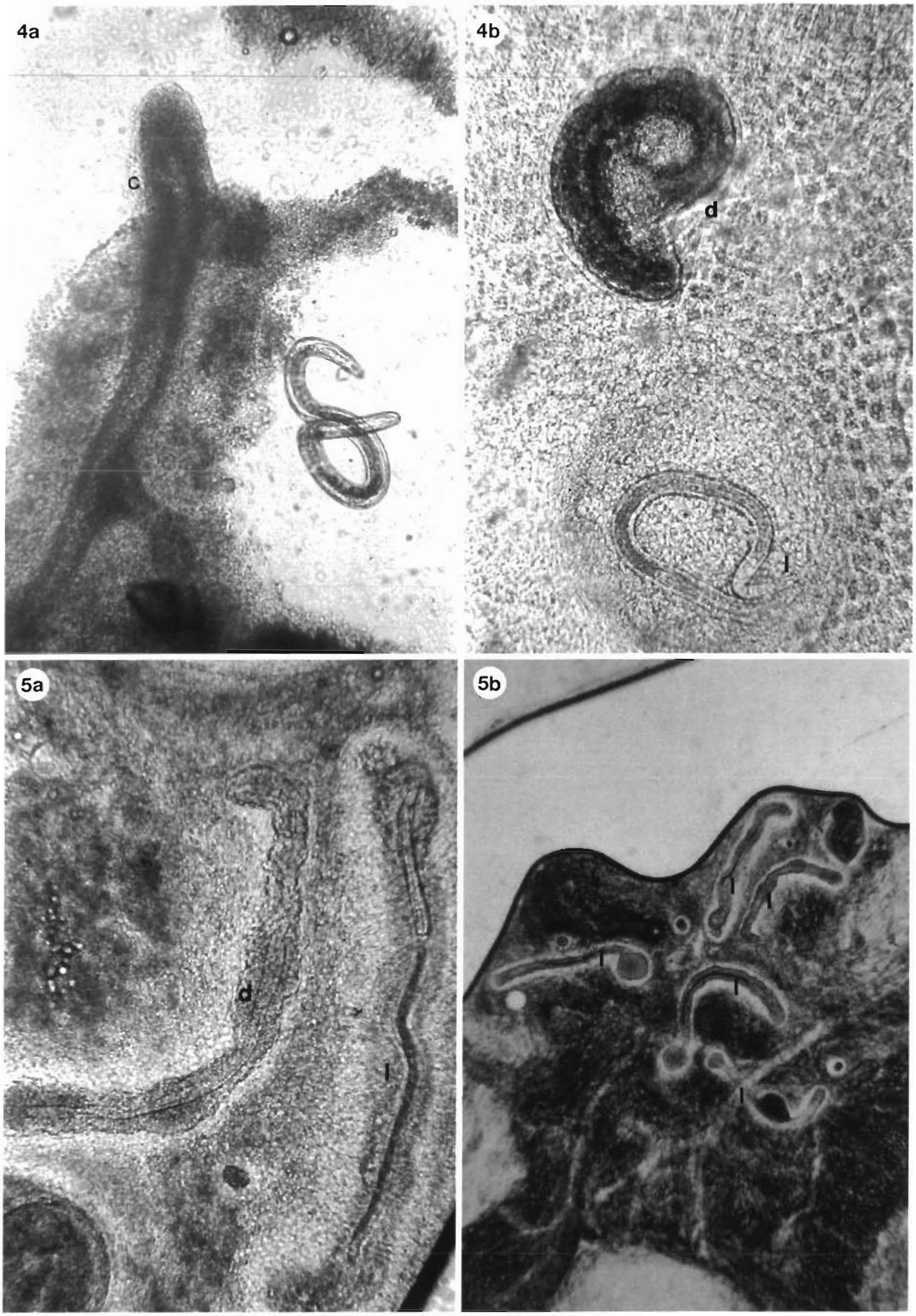
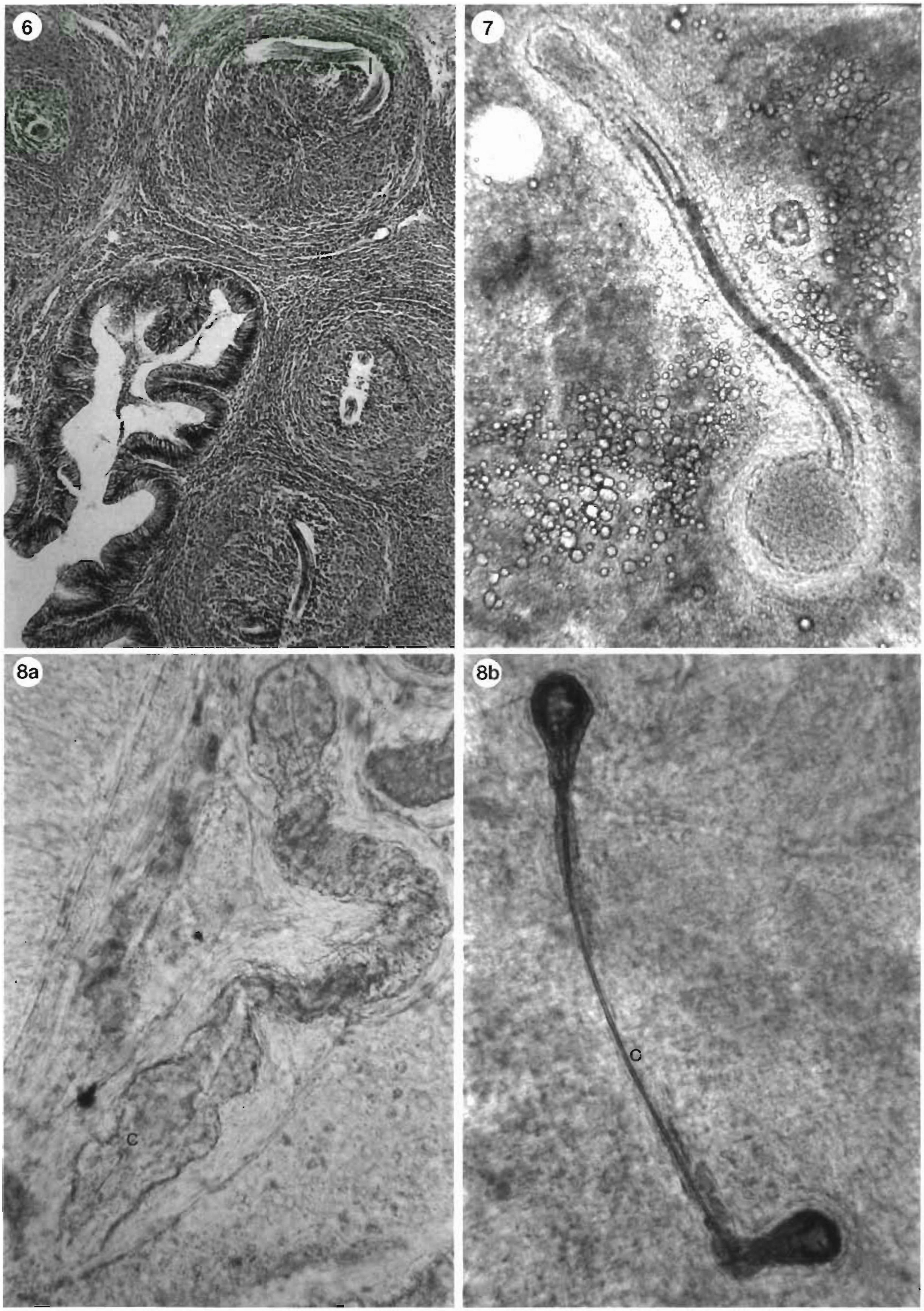


Fig 4 & 5. *Anguillicola crassus* Fig. 4. (a) Live L_3 larva leaving the capsule (c) in paratenic host. Fresh smear preparation, × 126. (b) Live (l) and dead (d) L_3 larvae in their capsules in paratenic host. Fresh smear, × 135. Fig. 5. (a) Elongated type of capsules with live (l) and dead (d) L_3 larvae in paratenic host Fresh smear, × 153 (b) Elongated type of capsules with larvae (l). Fresh smear, × 43



Figs. 6 to 8. *Anguillicola crassus*. Fig. 6. Spherical capsules (c) around L_3 larvae (l) on European catfish *Silurus glanis* fingerling's stomach. HE-stained histological section, × 135. Fig. 7. Freshly dead larva in its capsule. The structure is still very discernible. Fresh smear, × 153. Fig. 8. (a, b) Two types of decomposed encapsulated L_3 larvae in paratenic hosts. The cuticles (c) are still recognizable. Fresh smear, × 243 sent in the fish contained disrupted larvae with only the cuticle being recognizable (Fig. 8a, b).

DISCUSSION

Studies aimed at identifying the potential paratenic hosts of *Anguillicola crassus* have already been conducted. Interestingly enough, no such data are known from Asia, the original habitat of this nematode. Of the European authors dealing with the paratenic hosts of *A. crassus*, Cannaerts (1989) demonstrated larvae from 2 species (perch *Perca fluviatilis*, pumpkinseed *Lepomis gibbosus*), and Haenen & van Banning (1990) from 5 species (freshwater smelt *Osmerus eperlanus*, ruffe *Gymnocephalus cernuus*, perch *Perca fluviatilis*, pike perch *Stizostedion lucioperca*, three-spined stickleback *Gasterosteus aculeatus*). In Belgium, Thomas & Ollevier (1992) demonstrated larval infection in 16 paratenic host species belonging to 16 different taxonomical entities, and established that the prevalence of larval infection was higher in the physoclist than in the physostome species. Of the species which were found infected in Belgium, 9 also act as paratenic hosts of *A. crassus* in Lake Balaton: ruffe, pumpkinseed, pikeperch, perch, gudgeon, bleak, rudd, roach and tench. In Lake Balaton, 4 species (carp, gibel carp, bitterling, bream) found negative by Thomas & Ollevier (1992) were infected by 3rd stage larvae of *Anguillicola*. Six additional species hitherto not described as paratenic hosts proved to be infected by *A. crassus* larvae in Lake Balaton (asp, white bream, Chinese rasbora, pike, river goby, European catfish). *A. crassus* infection of high prevalence and intensity has already been described in the littoral zone of the Baltic Sea by Höglund & Thomas (1992) for black goby *Gobius niger*, a fish species taxonomically closely related to one of the newly recognized paratenic hosts, river goby.

In Lake Balaton, the bleak serves as the primary food source for eels. According to a 3 yr food structure study performed by Paulovits & Bíró (1987) between 1982 and 1984, the bleak represented 93.5 % of all food consumed by eels in the littoral zone and 31.9 % in the pelagic zone. Other fish species had a lower share in the food structure (1.5 % and 8.1 % in the littoral and the pelagic zone, respectively). Thus, if we compare the results reported by Paulovits & Bíró (1987) and our own findings presented here, it can be seen that eels of large body size may develop intensive infection with 40 helminths by consuming as few as 10 infected bleak specimens (with a mean live larval count of 4.1). In summer, an infection of such intensity is sufficient to produce swimbladder inflammation or thickening and, possibly, death. An infection of similar intensity may occur after the ingestion of a single ruffe specimen, as in the latter species the mean intensity of infection with live larvae was found to be 39.3.

Unfortunately, in recent years no one has studied the structure of food consumed by eels in Lake Balaton; thus, there are no data to support our observation that in the stomach of eels caught in the littoral zone the river goby was found in larger numbers than in the 1982 to 1984 survey of Paulovits & Bíró (1987) (0.3 %). This can be explained by the fact that only in 1970 did the river goby spontaneously establish itself in Lake Balaton (Bíró 1993), and only in the past few years has it become a really common species in the lake. In our opinion, after the bleak the river goby is the second most important species in the feeding of eels and, thus, it plays an important role in the life cycle of *Anguillicola crassus* in Lake Balaton, the more so as that paratenic host species is characterized by intensive infection by live larvae.

The question often arises why anguillicolosis occurring in Lake Balaton is peculiar, why eel mortalities comparable to that in Lake Balaton have not been reported from other European natural waters in which anguillicolosis emerged earlier, and why mostly eels of large body size died during the Lake Balaton eel mortality. The data presented in this paper furnish a partial answer to these questions. Lake Balaton has an overpopulated eel stock mostly comprising eels of large body size (Molnár et al. 1993). These eels, prevented from transmigrating, mainly feed on bleak, a fish species already showing uniform infection by *Anguillicola crassus* larvae. Thus, highly intensive *A. crassus* infection easily develops in the eels.

Some paratenic host species, which play a less important role in the food structure of Lake Balaton eels, may develop very intensive infection. Thomas & Ollevier (1992) and Höglund & Thomas (1992) have called attention to the fact that among the intensively infected paratenic hosts benthic species are dominant. This is supported by our observation made in Lake Balaton, where the benthic species (ruffe, river goby and European catfish) are the most intensively infected by live larvae. In the case of European catfish, however, not only the benthic habitude but also the accumulation of larvae resulting from the ingestion of other larva-infected paratenic hosts may have been responsible for the extremely intensive infection.

Although the present results are consistent with those obtained by Thomas & Ollevier (1992) for fishes from Belgian canals and support their opinion that physoclist fish species are better paratenic hosts than physostome species, we cannot consider the bleak an accidental host, as that species has the biggest share in the eel's food structure in Lake Balaton. The difference between the so-called good paratenic hosts and those less suitable for the larvae depends not so much on their infection by 3rd stage larvae as on the host reaction. Namely, in physoclist fishes the larvae seem to survive longer, and larval death and tissue reactions are less common than in physostome (primarily cyprinid) fishes in which dead larvae are more frequently found besides the live ones.

The ability of larvae to survive in paratenic hosts and the type of host reactions developing in such hosts differs by fish species in Lake Balaton. Still, it cannot be unequivocally stated that cyprinids (primarily the bleak) exhibiting a stronger host reaction are less important in the parasite's life cycle than the pikeperch which does not show a host reaction and was found to contain exclusively live larvae in this study. The fish species playing a role in the parasite's life cycle do not always coincide with those species which ensure the best and longest survival of larvae.

The high adaptability of *Anguillicola* larvae to new paratenic hosts indigenous only in Europe has probably greatly facilitated the spread of this parasite throughout the European continent. However, the example of Lake Balaton indicates that in the parasite's life cycle in different waters different fish species may act as primary paratenic host, depending on the feeding habits of eels in the given habitat.

Acknowledgements. I thank my project leader, Dr Kálmán Molnár, for his useful advice, and Ms Emese Papp and Ms Andrea Jávori for skilful technical assistance. Thanks also to the staff of the Limnological Research Institute of the Hungarian Academy of Sciences for their help in catching the fish used in this study. This work was carried out with financial support from the National Research Fund (OTKA), contract no. T 6035.

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Responsible Subject Editor: W. Körting, Hannover, Germany

Manuscript first received: July 5, 1993
Revised version accepted: October 6, 1993