FOLIA PARASITOLOGICA 43: 305-311, 1996

Experimental studies on the infectivity of *Anguillicola crassus* third-stage larvae (Nematoda) from paratenic hosts

Csaba Székely

Veterinary Medical Research Institute, Hungarian Academy of Sciences, H-1143 Budapest, Hungária krt. 21, Hungary

Key words: *Anguillicola crassus*, experimental infection, larval stages, intermediate hosts, paratenic hosts, European eel, host reaction

Abstract. The swimbladder parasite *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 (Nematoda: Dracunculoidea) is a well-known pathogenic parasite of the Japanese and European eels. Numerous studies on the life cycle of the parasite have revealed the involvement of a copepod or an ostracod intermediate host and a fish paratenic host, in which the third-stage larvae (L_3) infective to the eel develop. The present study comprised infection experiments with the larvae of *A. crassus*. These experiments can be divided into three groups: (1) experimental reproduction of the parasite's life cycle via copepod intermediate hosts and fish paratenic hosts, (2) infection of another potential paratenic host with third-stage larvae of *A. crassus* collected from a paratenic host; (3) study of the ability of larvae damaged by paratenic hosts to infect the final host, the eel. Infection experiments have revealed that larvae which are still viable but have become encapsulated as a result of the host reaction mounted against them by cyprinid paratenic hosts (bleak, *Alburnus alburnus*) have lost their ability to infect the final host, the eel. At the same time, experimental infection of the eel with larvae derived from other paratenic fish hosts (river goby, *Neogobius fluviatilis*; ruffe, *Gymnocephalus cernua*) showing no or only weak host reaction proved to be successful.

The nematode *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 parasitises the swimbladder lumen of the European eel (*Anguilla anguilla* L.). It infects Japanese and European eels, but appears to be pathogenic in European eels only, in Europe and Japan. It has recently been reported also from the American eel, *Anguilla rostrata*, from the southern part of the USA (Johnston et al. 1995). It was brought into Europe in the early 1980's, and then rapidly spread throughout the continent. The parasite was first detected in Germany (Neumann 1985). Detailed data on its prevalence and incidence in Europe have been reported by Køie (1991) and Moravec (1992). The literature is relatively abundant in data on the development of *A. crassus*. Apart from a few early studies made in Asia (Hirose et al. 1976, Egusa 1979), this question has mainly been dealt with by European authors (Haenen et al. 1989, Petter et al. 1989, De Charleroy et al. 1990, Kennedy and Fitch 1990). Like the related species *A. globiceps* Yamaguti, 1935 known from the Far East, *A. crassus* has been found to develop with the participance of a copepod (Cyclopidae or Ostracoda) acting as intermediate host, which becomes infected with second stage larvae which then develop into third-stage infective larvae (L_3) within the intermediate host. Eels become infected by ingesting the infected copepods. In the eel's swimbladder wall the larvae develop further into 4th-stage (preadult) larvae (L_5) which then reach their maturity in the swimbladder lumen. Although this life cycle pattern is undoubtedly a valid one, the studies of Cannaerts (1989), Haenen and van Banning (1990), Höglund and Thomas (1992), Thomas and Ollevier (1992), Pazooki and Székely (1994) and Székely (1994,1995) have called attention to the fact that under natural conditions the eel, a fish species which rarely feeds on plankton, becomes infected via paratenic hosts. Results obtained to date indicate that only eel species can act as the final host for *A. crassus*; however, practically all fish species are potential paratenic hosts of that parasite. Haenen and van Banning (1990) recorded 5, Thomas and Ollevier (1992) 16, while Székely (1994, 1995) 20 and 22 fish species, respectively, acting as paratenic hosts for *A. crassus*. The transmission of infection from paratenic fish hosts to the eel has been demonstrated experimentally by Haenen and van Banning (1991) and Moravec and Konecny (1994). Thomas and Ollevier (1992) reported marked differences in the incidence of *A. crassus* larvae in different paratenic host species: they detected the larvae much more frequently in percid fishes and gobies than in cyprinids, and pointed out that in the perch third-stage larvae occurred together with fourth-stage larvae and preadult forms.

Data on the viability of *Anguillicola* larvae in paratenic hosts have been published by Thomas and Ollevier

(1992), Pazooki and Székely (1994) and Székely (1994, 1995) who demonstrated that in certain fish species (e.g. river goby) the larvae survive much longer than in other species. Histological studies on the type of host reaction mounted against the larvae in paratenic hosts have been carried out by Székely et al. (1996).

This paper reports the results of infection experiments carried out with the second- and third-stage larvae of *A. crassus*. These experiments can be arranged into three groups: (1) Reproduction of the life cycle in the known way (through copepod intermediate hosts and fish paratenic hosts); (2) production of larval infection in a potential paratenic host with third-stage larvae collected from another paratenic host species; (3) studies on whether the host reaction (encapsulation of larvae) developing in certain paratenic fish hosts (e.g. bleak) can affect the ability of larvae to infect the final host (i.e. the eel).

MATERIALS AND METHODS

1. Experiments to infect intermediate hosts and potential paratenic hosts and to study the host reaction mounted by them against the larvae (Table 1)

The second-stage larvae of *Anguillicola crassus* used in the experiments were collected from the swimbladder of eels caught from Lake Balaton, and then fed to copepods belonging to the genera *Cyclops* and *Diaptomus* (not identified more closely). During the experiments the copepods were kept in aquaria pretreated with rabbit manure. A total of 4 experiments were performed. After 15–24 days the copepod stocks were examined for the presence of third-stage larvae of *A. crassus*; if such larvae had developed in them, the copepods were fed to different potential paratenic fish hosts (marmoured goby, *Proterorhinus marmoratus* Pallas, 1811; bleak, *Alburnus alburnus* Linnaeus, 1758; common carp, *Cyprinus carpio* Linnaeus, 1758; goldfish, *Carassius auratus auratus* Linnaeus, 1758) of small size (4–7 cm). The fish were assigned to groups of 5–20 individuals each, and monitored for the development of host reaction by dissection in the period between 3–178 days post infection (DPI). Some of these small fish (marmoured goby, bleak) were obtained from waters where no anguillicolosis had yet occurred, while others (common carp, goldfish) were cultured in a parasite-free manner in aquaria.

Evaluation of the experiments was done by light-microscopic examination of squash preparations made from the abdominal organs of the fish between two slides.

2. Experiments to infect potential paratenic hosts with *Anguillicola crassus* larvae collected from other paratenic hosts living in Lake Balaton (Table 2)

For these experiments, third-stage larvae of *A. crassus* located on the outer surface of the gut and unaffected by the host reaction were collected by dissection under microscope from river gobies (*Neogobius fluviatilis* Pallas, 1811) living in Lake Balaton. These larvae, together with pieces of the infected gut, were fed to common carp fry reared parasite free in the laboratory. The pieces of gut were offered individually with tweezers. The mean number of larvae fed to one fish was 38, 30, and 35 in the different experiments. Common carp fry were killed 6, 17 and 21 DPI and fresh preparations made from their abdominal organs were examined for the presence of *Anguillicola* larvae under microscope.

3. Experiments to infect the final host (European eel) with different types (free or encapsulated) larvae collected from fish paratenic hosts (Table 3)

The eels used in the study had been derived from the *Anguillicola*-free stock of the Hévíz eel farm. These eels were infected with third-stage larvae of *A. crassus* collected from Lake Balaton fish of 5–8 cm body length. The larvae used for infection included encapsulated live larvae collected from bleak and free live larvae collected from ruffe (*Gymnocephalus cernua* Linnaeus, 1758) and river goby. As larvae occurred on the outer surface of the gut in the highest number, only larvae found in such a location were used for infection. After gently squashing the infected gut segments between slides, the larvae were counted under microscope. The infected intestinal segments were suspended in 0.65 % saline solution and injected into the eels' stomach via a tube, without anasthetising the eels. The infective dose was 10–100 larvae per eel. The larvae administered to each eel had usually been collected from several specimens of a given paratenic host species. A total of 19 eels were infected (6, 5 and 8 with larvae collected from bleak, ruffe and river goby, respectively). The eels were killed between 22 and 97DPI and their swimbladders were examined for the presence of *Anguillicola* larvae as well as preadult and adult stages.

RESULTS

1. Experiments to infect intermediate hosts and potential paratenic hosts and to study the host reaction mounted by them against the larvae (Table 1)

Anguillicola crassus larvae were consistently detected in the *Cyclops* and *Diaptomus* intermediate hosts used for the experiments 15, 16, 17 and 24 DPI. The average prevalence of infection was 5–10 %, while its intensity was variable: in experiments 1, 3 and 4 a lower intensity (1–2 larvae per infected copepod; marked + in the table), whereas in experiment 2 a higher intensity of infection was observed (1–4 larvae per infected copepod; marked ++ in the table). By feeding infected copepods to paratenic host fish of small size, infection by third-stage larvae was successfully established in all fish species used (marmoured goby, bleak, common carp, goldfish). In cyprinids, host reaction against the larvae was demonstrable soon after infection. Death of the larvae could be observed also in the common carp. In the bleak, which also belongs to cyprinids, the

Table 1. Infection experiments with second and third-stage larvae of *Anguillicola crassus* in some intermediate and paratenic hosts.

Intermediate hosts				Paratenic hosts						
No. of experiment	Intermediate host used	Duration of experiment (days)	Intensity of infection	Species of infected fish	Duration of experiment (days)	Prevalence* of infection	Intensity of infection with larvae			
							free live	enc. live	free dead	enc.dead
1	*Cyclops* sp.	17	+	*Proterorhinus marmoratus*	20	2/10	1, 2	–	–	–
			+		60	3/10	1, 3, 3	–	–	–
2	*Cyclops* sp.	16	2+	*Alburnus alburnus*	3	1/1	1	–	–	–
					19	1/1	–	6	–	–
					31	0/1	–	–	–	–
					67	1/1	1	2	–	–
					87	1/1	–	2	–	3
					178	0/1	–	–	–	–
						4/6				
				Cyprinus carpio	3	1/1	15	–	–	–
					19	0/1	–	–	–	–
					31	1/1	1	–	–	–
					67	0/1	–	–	–	–
					87	1/2	–	–	–	4
					178	1/2	–	–	–	7
						4/8				
				Carassius auratus auratus	3	1/1	10	–	–	–
					19	1/1	2	–	–	–
					31	1/1	–	–	5	–
					67	1/1	–	–	1	–
					87	1/1	–	1	–	–
					178	2/4	1, 2	–	–	–
						7/9				
3	*Cyclops* sp.	15	+	*Cyprinus carpio*	35	1/3	–	–	–	1
					89	0/2	–	–	–	–
						1/5				
				Carassius auratus auratus	35	2/3	1, 2	–	–	1, 2
					89	0/1	–	–	–	–
						2/4				
4	*Diaptomus* sp.	24	+	*Alburnus alburnus*	85	**6/8**	–	1, 1, 2, 3	–	2, 3

* number of infected fish / number of all fish examined

encapsulation of larvae had taken place already by 19 DPI, and a proportion of the encapsulated larvae had died by 87 DPI. It was interesting that in another cyprinid, the goldfish, an encapsulated but still living larva was found only on a single occasion, while in two cases death of the larvae took place without a cellular host reaction. Twenty days after infection only live larvae were found in the marmoured goby, the species representing gobies in this experiment.

2. Experiments to infect potential paratenic hosts with *Anguillicola crassus* larvae collected from other paratenic hosts living in Lake Balaton (Table 2)

The feeding of free live larvae collected from river goby to common carp resulted in larval infection of the "second" paratenic host in 2 out of the 3 experiments. Cellular reaction against the larvae was rapid: thus, on day 6 encapsulated but still living larvae were observed

Table 2. Experiments to infect a paratenic host with *Anguillicola crassus* larvae from another paratenic host.

No. of experiment	Origin	No. per exposed fish	Type of 3rd-stage larvae	Species	No. of exposed fish	Method of exposure	Time between exposure and examination	Prevalence of infection	Intensity of infection with larvae			
									free live	enc.* live	free dead	enc. dead
1	*Neogobius fluviatilis*	38	free	*Cyprinus carpio*	2	feeding	6 days	2/2	2	3	1	–
2		35			5		21 days	2/5	2	–	–	1
3		30			5		17 days	0/5	–	–	–	–

* enc. = encapsulated

while on day 21 encapsulated dead larvae were detected.

3. Experiments to infect the final host (European eel) with different types (free or encapsulated) larvae collected from paratenic fish hosts (Table 3 and Fig. 1)

Six eels were administered, through a gastric tube, live encapsulated third-stage larvae of *A. crassus* collected from the bleak (10, 12, 19, 24, 26 and 35 larvae, respectively). The infection was not successful in any of these cases. At dissection carried out 22–71 DPI neither larvae in the swimbladder wall nor adult stages in the swimbladder lumen were found. No larvae were found in the intestinal wall of dissected eels (Table 3, experiments 1–6).

The infection of 5 eels, through a gastric tube, with free live larvae collected from the ruffe yielded the following results. The eels infected with 20 and 28 larvae remained negative, while those infected with 51, 95 and 100 larvae were found to harbour 2, 7 and 5 adult and preadult *A. crassus* stages, respectively, in the swimbladder at dissection carried out 45–56 DPI (Table 3, experiments 7–11).

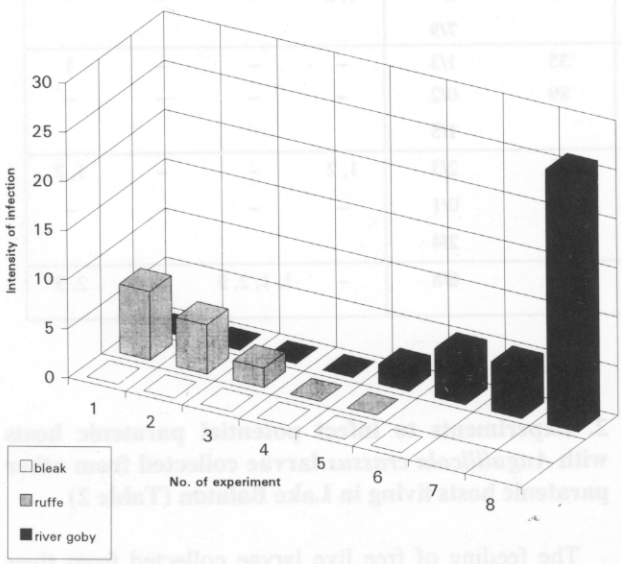

Fig. 1. Experiments to infect the final host (the European eel) with third-stage larvae of *Anguillicola crassus* of different status (free or encapsulated), collected from fish paratenic hosts.

Eight eels were infected, through a gastric tube, with 8, 12, 20, 30, 55, 55, 58 and 89 free live larvae, respectively, collected from the river goby. *Anguillicola* infection was demonstrable in 4 out of the 8 eels (50 %) 29–97 DPI. The intensity of infection was as follows: on 75 DPI with 8 larvae 5 adult stages, on 56 DPI with 30 larvae 4 adult stages, 3 preadult stages, 10 L_4 and 9 L_3, on 29 DPI with 55 larvae 2 L_4, while on 60 and 97 DPI after two infections with a total of 89 larvae 5 adult helminths were found (Table 3, experiments 12–19).

DISCUSSION

The life cycle of *Anguillicola crassus* has successfully been reproduced under experimental conditions by several researchers (Haenen et al. 1989, De Charleroy et al. 1990, Haenen and van Banning 1991, Moravec et al. 1993, 1994, Haenen et al. 1994, Moravec and Konecny 1994). Therefore, the infection of *Cyclops* and *Diaptomus* species in the first group of the experiments (Table 1), and the production of larval infection in potential paratenic fish hosts by feeding them infected copepods represented a verification of earlier works and was designed to experimentally corroborate the observation made in natural waters, i.e. that differences exist between paratenic host species of *A. crassus* in the type and speed of host reaction against the larvae (Székely 1994, 1995, Székely et al. 1996).

According to De Charleroy et al. (1990), the third-stage larvae of *A. crassus* retain the ability to move freely in the abdominal cavity of experimentally infected common carp and ide (*Leuciscus idus* Linnaeus, 1758) for a long period. This statement is at variance with the observation of Petter et al. (1989), who reported that in guppy (*Poecilia reticulata* Peters, 1859) the larvae became surrounded by a thin capsule. The latter observation is supported by the experimental findings by Moravec and Konecny (1994), who reported

Table 3. Experiments to infect the final host (European eel) with third-stage larvae of *Anguillicola crassus* of different status (encapsulated or free), collcted from paratenic hosts. One eel (*Anguilla anguilla*) was challenged in each experiment using a syringe.

No. of experiments	Type (and origin)of 3rd-stage larvae	No. of 3rd-stage larvae used	Time between exposure and examination (days)	Prevalence of infection in eel	Intensity of infection in eel			
					adult	preadult	L_4	L_3
1	Encapsulated (*Alburnus alburnus*)	10	26	0/1	–	–	–	–
2		12	58	0/1	–	–	–	–
3		19	31	0/1	–	–	–	–
4		24	22	0/1	–	–	–	–
5		26	59 and 71	0/1	–	–	–	–
6		35	67	0/1	–	–	–	–
7	Free (*Gymnocephalus cernua*)	20	55	0/1	–	–	–	–
8		28	56	0/1	–	–	–	–
9		50	45	1/1	2	–	–	–
10		95	55	1/1	5	2	–	–
11		100	45	1/1	2	3	–	–
12	Free (*Neogobius fluviatilis*)	8	75	1/1	5	–	–	–
13		12	55	0/1	–	–	–	–
14		20	79	0/1	–	–	–	–
15		30	56	1/1	4	3	10	9
16		55	59	0/1	–	–	–	–
17		55	29	1/1	–	–	2	–
18		58	79	0/1	–	–	–	–
19		89	60 – 97	1/1	5	–	–	–

that in different (primarily cyprinid and live-bearing toothcarps) paratenic host species (*Alburnus alburnus*, *Gobio gobio*, *Poecilia reticulata*) the majority of *A. crassus* larvae were alive but surrounded by a thin connective tissue capsule one month after experimental infection. The present author's own observations (i.e. that in bleak live but encapsulated larvae were found as early as 19 days after infection, while in common carp and goldfish dead encapsulated larvae were first recorded on 35 and 87 DPI, respectively) are consistent with the latter findings.

During our studies on fish species of Lake Balaton we observed that encapsulation of larvae and host reaction did not develop against *A. crassus* larvae found e.g. in the river goby, as opposed to those occurring in cyprinids (Székely 1994, 1995, Székely et al. 1996). This finding is supported by the results of experimental infection of another goby species, the marmoured goby, with *A. crassus* larvae: in that case, the larvae were moving freely in the abdominal cavity even 20–60 days after infection, and no cellular host reaction was detectable.

The second group of experiments (Table 2) addressed questions that had not been studied previously. Larvae transferred from a paratenic host species failing to mount a host reaction against larvae (the river goby) to a cyprinid species showing a strong host reaction (common carp) seem to induce a much faster host reaction in the paratenic host, common carp, than if that fish species were infected directly by feeding on the intermediate host, *Cyclops* sp., infected by larvae (Table 2). These experiments also revealed that larvae transmitted from one paratenic host species to another maintain their viability. This mechanism must have been responsible for the accumulation of larvae observed in natural waters (Székely 1994) primarily in predatory fish species acting as a paratenic host (European catfish, *Silurus glanis*).

The speed of the host reaction mounted to *A. crassus* larvae varies with paratenic host species. Before this study, this fact had been known only from the dissection results of naturally infected fish (Székely et al. 1996). The third part of this study (Table 3) furnished evidence supporting our earlier findings, i.e. that in no case could anguillicolosis be produced by infecting eels with a large number of encapsulated but still living larvae collected from a cyprinid species, namely the bleak. At the same time, eels could be infected successfully on several occasions with free live larvae collected from the ruffe and the river goby, and were found to harbour

both adult and larval stages of *A. crassus*. However, contrary to expectations, the dissected eels contained far fewer helminths than the number of larvae used for infection. This may be due to the host reaction which takes place in the eel during larval migration starting from the gut; as a result of that reaction, only some part of the larvae survive and reach the swimbladder.

The results of these experiments support our earlier hypothesis that both "good" and "less suitable" paratenic hosts may be involved in the life cycle of *A. crassus* in natural waters. Thus, as a result of the rapid host reaction occurring in cyprinids not only the dead but also the already encapsulated but still living larvae fail to infect the eel. In the littoral zone of Lake Balaton the bleak serves as the primary food source for eels (Paulovits and Bíró 1987). Due to the rapid anti-larval host reaction taking place in the bleak, it is highly probable that bleak can transmit anguillicolosis to the definitive eel host only if they have a fresh larval infection established a few days ago, and primarily in the warm season. The situation is different with the river goby, a species which also lives primarily in the littoral zone. *A. crassus* larvae survive for a long period in the river goby and thus can produce anguillicolosis in the feeding eels throughout the year. Although the river goby is much less important as a food source for eels than the bleak (Paulovits and Bíró 1987), based upon the present findings and also because of the gradual increase of its population in Lake Balaton (Bíró 1995) it seems to play a much more important role in the development and severity of anguillicolosis in Lake Balaton than could be expected on the basis of its proportion in the eel's diet. The same applies to the ruffe, a species living primarily in the pelagic zone. This "good paratenic host" also plays a bigger role in the development of anguillicolosis than could be expected from its role as a food source for the eel.

As a general conclusion, it can be stated that the present studies have provided experimental evidence that certain fish species (gobies, ruffe) act as "good" paratenic hosts for *A. crassus* while others (cyprinids) are less suitable paratenic hosts for that nematode. Naturally, it is always the species composition of fish living in a given habitat that determines which species are the most favourable paratenic hosts in the life cycle of *A. crassus* at a specific moment in time.

Acknowledgments. This work was supported by the National Research Fund (OTKA) of Hungary (projects no. T 6035 and T 020044) and by the Fish Management Fund of the Ministry of Agriculture. The author thanks Ms. Emese Papp for her help provided in carrying out the experiments and in fish collection, and Dr. Kálmán Molnár for valuable advice regarding the experiments. Thanks are also due to the Balaton Fisheries Company for having provided *Anguillicola*-free eels for the experiments free of charge.

REFERENCES

BÍRÓ P. 1995: Food and growth of the river goby (*Neogobius fluviatilis* Pallas) in the littoral zone of Lake Balaton. In: Biomonitorozás-Biodiverzitás (Biomonitoring – Biodiversity). Book of Proceedings. XXXVII. Hidrobiológus Napok (XXXVIIth Hydrobiological Days), 20–22 Sept. 1995, Tihany, Hungary, pp. 27–30. (In Hungarian.)

CANNAERTS V. 1989: Interactie van *Anguillicola crassus*, met enkele typishe reservoirgastheren en de eindgastheer, *Anguilla anguilla*. MSc Thesis, Catholic University of Leuven.

DE CHARLEROY D., GRISEZ L., THOMAS K., BELPAIRE C., OLLEVIER F. 1990: The life cycle of *Anguillicola crassus*. Dis. Aquat. Org. 8: 77–84.

EGUSA S. 1979: Notes on the culture of the European eel (*Anguilla anguilla* L.) in Japanese eel farming ponds. Rapp. P-v. Réun. Cons. int. Explor. Mer. 174: 51–58.

HAENEN O. L. M., GRISEZ L., DE CHARLEROY D., BELPAIRE C., OLLEVIER F. 1989: Experimentally induced infections of European eel *Anguilla anguilla* with *Anguillicola crassus* (Nematoda, Dracunculoidea) and subsequent migration of larvae. Dis. Aquat. Org. 7: 97–101.

HAENEN O. L. M., VAN BANNING P. 1990: Detection of larvae of *Anguillicola crassus* (an eel swimbladder nematode) in freshwater fish species. Aquaculture 87: 103–109.

HAENEN O. L. M., VAN BANNING P. 1991: Experimental transmission of *Anguillicola crassus* (Nematoda, Dracunculoidea) larvae from infected preyfish to the eel, *Anguilla anguilla*. Aquaculture 92: 115–119.

HAENEN O. L. M., WIJNGARDEN T. A. M., BORGSTEEDE F. H. M. 1994: An improved method for the production of infective third-stage juveniles of *Anguillicola crassus*. Aquaculture 123: 163–165.

HIROSE H., SEKINO T., EGUSA S. 1976: Notes on the egg deposition, larval migration and intermediate host of the nematode *Anguillicola crassa* parasite in the swimbladder of eels. Fish Pathol. 11: 27–31. (In Japanese, with English abstract.)

HÖGLUND J., THOMAS K. 1992: The black goby, *Gobius niger*, as a potential paratenic host for the parasitic nematode *Anguillicola crassus* in a thermal effluent of the Baltic. Dis. Aquat. Org. 13: 175–180.

JOHNSTON S. K., FRIES L. T., WILLIAMS J., HUFFMAN D. G. 1995: Presence of the parasitic swim bladder nematode, *Anguillicola crassus*, in Texas aquaculture. World Aquaculture 26: 35-36.

KENNEDY C. R., FITCH D. J. 1990: Colonization, larval survival and epidemiology of the nematode *Anguillicola*

crassus, parasitic in the eel, *Anguilla anguilla*, in Britain. J. Fish Biol. 36: 117–131.

KØIE M. 1991: Swimbladder nematodes (*Anguillicola* spp.) and gill monogeneans (*Pseudodactylogyrus* spp.) parasitic on the European eel (*Anguilla anguilla*). J. Cons. int. Explor. Mer. 47: 391–398.

MORAVEC F. 1992: Spreading of the nematode *Anguillicola crassus* (Dracunculoidea) among eel populations in Europe. Folia Parasitol. 39: 247–248.

MORAVEC F., DI CAVE D., ORECCHIA P., PAGGI L. 1993: Studies on the development of *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974(Nematoda: Dracunculoidea) in the intermediate host. Folia Parasitol. 40: 39–48.

MORAVEC F., KONECNY R. 1994: Some new data on the intermediate and paratenic hosts of the nematode *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 (Dracun- culoidea), a swimbladder parasite of eels. Folia Parasitol. 41: 65–70.

MORAVEC F., DI CAVE D., ORECCHIA P., PAGGI L. 1994: Experimental observations on the development of *Anguillicola crassus* (Nematoda: Dracunculoidea) in its definitive host, *Anguilla anguilla* (Pisces). Folia Parasitol. 41: 138–148.

NEUMANN W. 1985: Schwimmblasenparasit *Anguillicola* bei Aalen. Fischer und Teichwirt 36: 322.

PAULOVITS G., BÍRÓ P. 1987: Feeding and growth of the eel in Lake Balaton. In: Proc. 29th "Georgikon" Days, 25–26 August 1987, Keszthely, Hungary, pp. 213–226. (In Hungarian, with English abstract.)

PAZOOKI J., SZÉKELY Cs. 1994: Survey of the paratenic hosts of *Anguillicola crassus* in La Velence, Hungary. Acta Vet. Hung. 42: 87–97.

PETTER A. J., FONTAINE Y. A., LE BELLE N. 1989: Étude du dévelopment larvaire de *Anguillicola crassus* (Dracunculoidea) chez un Cyclopidae de la région parisienne. Ann. Parasitol. Hum. Comp. 64: 347–355.

SZÉKELY Cs. 1994: Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary. Dis. Aquat. Org. 18: 11–20.

SZÉKELY Cs. 1995: Dynamics of *Anguillicola crassus* (Nematoda: Dracunculoidea) larval infection in paratenic host fishes of Lake Balaton, Hungary. Acta Vet. Hung. 43: 401–422.

SZÉKELY Cs., PAZOOKI J., MOLNÁR K. 1996: Host reaction in paratenic fish hosts against 3rd stage larvae of *Anguillicola crassus*. Dis. Aquat. Org. 26: 173–180.

THOMAS K., OLLEVIER F. 1992: Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. Dis. Aquat. Org. 13: 165–174.

Received 10 April 1996

Accepted 29 May 1996