

Dynamics of *Anguillicola crassus* larval infections in a paratenic host, the ruffe (*Gymnocephalus cernuus*) from the Oder River on the border of Germany and Poland

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Abstract

The course of infection of 2-year-old ruffe (*Gymnocephalus cernuus* L.) from the Oder River (Germany/Poland) with third-stage larvae (L3) of *Anguillicola crassus* (Nematoda: Anguillicolidae) was investigated at monthly intervals between March 1994 and March 1995. Of 230 fish examined, 152 (66%) harboured viable L3. Monthly prevalences fluctuated between 12 and 96%; mean intensities ranged from 1.0 to 5.6 L3 per infected fish. Temperature-dependent differences in infection were noted with the prevalence and mean intensity of infection being significantly higher (Chi-Square test and Mann-Whitney-U-test, respectively; $P < 0.01$) at water temperatures less than 10°C (cold period) than at those above (warm period). These differences remained significant even after the division of fish samples into two size classes (8.5–10.5 cm, 11–13 cm). Although the paratenic hosts may acquire infections year round, the results suggest that ruffe become infected mainly during the cold season and that the host's feeding ecology determines the final course of infection.

Introduction

In Europe, the dracunculoid nematode *Anguillicola crassus* rapidly became a common parasite of European eel, *Anguilla anguilla* (Moravec, 1992) after its introduction in the early 1980s (Neumann, 1985) from Southeast Asia, where it also infects the Japanese eel, *A. japonica* (Kuwahara *et al.*, 1974). The rapid spread of this parasite has been studied with concern as it causes severe pathology in its definitive host (van Banning & Haenen, 1990; Molnar *et al.*, 1993). The easy colonization of new habitats by *Anguillicola crassus* is supported by its relatively simple life cycle which comprises only two hosts. Adult nematodes parasitize the swimbladder lumen of eels where gravid females deposit eggs containing fully developed second-stage larvae (L2). According to Hirose *et al.* (1976), the L2 hatch from the eggs, penetrate through the ductus pneumaticus in to the

intestine and pass into the water along with the faeces. Hatching of the L2 may also take place in the intestinal tract or in water (De Charleroy *et al.*, 1990; Moravec *et al.*, 1993; Thomas & Ollevier, 1993). Numerous cyclopoid copepod species (see Moravec, 1994) as well as certain ostracods and calanoid copepods (Petter *et al.*, 1990; Hartmann, 1994; Moravec & Konecny, 1994) can act as intermediate hosts, where ingested nematodes migrate into the haemocoel and moult to infective third-stage larvae (L3). Eels acquire infection by eating infected copepods. Alternatively, eels can become infected while feeding on small fish that serve as paratenic hosts that ingest infected copepods (De Charleroy *et al.*, 1990; Haenen & van Banning, 1991).

Although the biology of *A. crassus* is well known and the influence of environmental factors on individual development and population dynamics has been extensively studied (see Moravec, 1994 and references therein), there is, however, only limited information on seasonal occurrence of larval *A. crassus* in its paratenic hosts (Thomas & Ollevier, 1992a; Székely, 1995) which are considered as important if not the main source of

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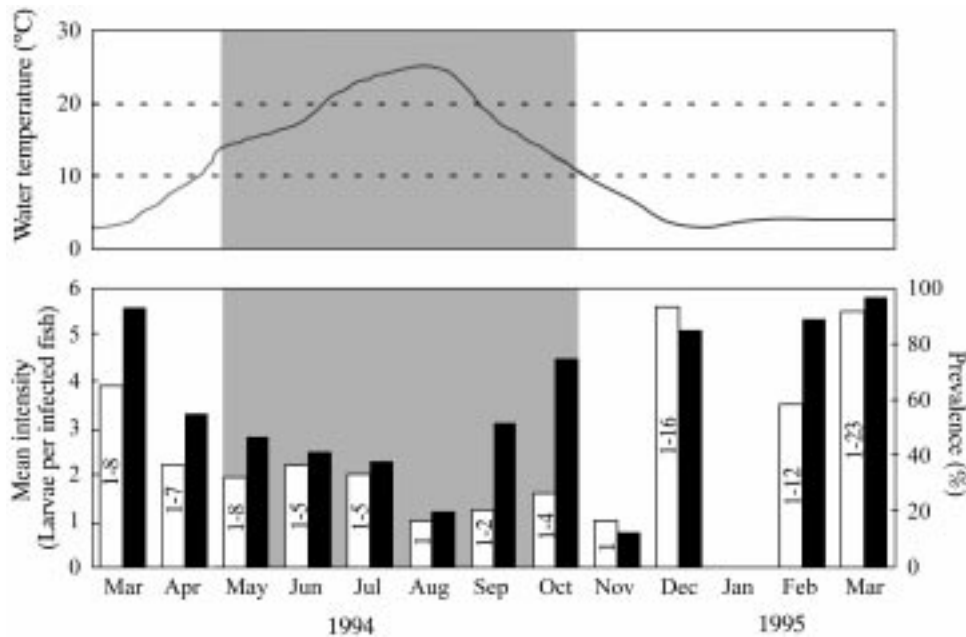


Fig. 1. Water temperatures in the Oder River and the prevalence (■) and mean intensity (□) of infection of 2/2+ ruffe (*Gymnocephalus cernuus*) with *Anguillicola crassus* third-stage larvae (L3) between March 1994 and March 1995. The warm period with water temperatures above 10°C is indicated by the grey background; numbers within the columns give the range of L3. No ruffe of the 2/2+ age class was caught in January 1995.

infection of eels (Székely, 1994, 1996; Lehmann *et al.*, 1996). During investigations on the ecology of endohelminths in ruffe (*Gymnocephalus cernuus*) from the Oder River (Germany/Poland), *A. crassus* larvae were regularly found embedded in the swimbladder wall (Pietrock, 1998). The present study consists of an analysis of the intraannual dynamics of *A. crassus* in 2-year-old ruffe from the Oder River to help explain differences in *A. crassus* population dynamics in eel final hosts from different localities.

Materials and methods

The sampling area is described in detail by Pietrock (1998). Briefly, the Oder River is situated in central Europe and forms at its lower part the border between Germany and Poland. Samples were taken between the river-km 695 and 699, i.e. near the town of Schwedt (Germany). In this region, the river is approximately 200–300 m wide and 3–5 m deep. Due to the intensity of primary production the water is characterized as eutrophic. The

Table 1. Number and morphometrical data of *Gymnocephalus cernuus* from the Oder River examined between March 1994 and March 1995.

Year and month	Number of fish examined	Mean total body length (mm) ± SD	Mean body weight (g) ± SD
1994 March	31	117 (11)	20.6 (6.0)
April	18	120 (12)	22.8 (8.1)
May	34	115 (9)	18.7 (3.9)
June	17	112 (13)	16.5 (4.5)
July	13	106 (11)	14.6 (5.2)
August	5	103 (4)	14.8 (2.5)
September	25	105 (10)	16.4 (3.8)
October	20	107 (10)	14.8 (3.4)
November	8	110 (10)	17.0 (5.8)
December	14	126 (4)	27.8 (6.0)
1995 February	17	111 (14)	17.1 (6.8)
March	28	117 (11)	21.0 (5.8)
Cold period	116	120 (10)	21.1 (7.0)
Warm period	114	110 (10)	16.5 (4.2)
Total	230	113 (12)	18.8 (6.2)

river bottom consists of sand and mud is polluted in part by heavy metals (Meinelt *et al.*, 1997).

From March 1994 to March 1995 a total of 266 ruffe were sampled monthly by means of traps and seines. On the same day of fish sampling, the water temperature was measured using a U-10 Water Quality Checker (Horiba, Ltd, Japan) at a distance of approximately 5 m from the shoreline and a depth of 2 m. After capture, fish were transported alive to the laboratory and were maintained in plastic holding tanks. Prior to dissection, which occurred within 48 h, the total body length and weight of fish were determined. Their ages, estimated from scales, ranged from 1+ to 3+ (Pietrock, 1998). Organs examined by means of a stereomicroscope included gills, eyes, muscle, liver, spleen, mesentery, swimbladder, kidneys, heart, brain and the gastrointestinal tract. The helminth parasites found were counted, and identified according to Bauer (1987) and Moravec (1994).

To test for seasonal differences in the infection of ruffe, the sampling period was divided into a warm (water temperature above 10°C) and a cold (water temperature below 10°C) season. The division at 10°C was used as it has been shown that this temperature is important for the onset of helminth infections in ruffe (Pietrock, 1998; Pietrock *et al.*, 1999b) and development of larval *A. crassus* in its final host, respectively (Knopf *et al.*, 1998).

Because 90% of fish caught belonged to the 2/2+ age class and thus no meaningful statistical comparisons within and between younger and/or older fish could be made, the analysis was focused on the 2/2+ age class, generating a sample size of 230 fish (table 1). To take into account differences in fish length between the 2-year-old and the 2+ ruffe, and potential size related effects on *A. crassus* infection, both the summer and winter 'cohorts' were divided into two size classes (8.5–10.5 cm; 11–13 cm) each.

Terminology is used according to Bush *et al.* (1997). Differences in the prevalence and mean intensity between the groups of fish collected during warm and cold seasons, and between different size classes were tested by means of the Chi-Square test (Pearson) and Mann-Whitney-U-test, respectively, using SPSS version 9.0.1 (SPSS Inc. 1999). Differences were considered statistically significant at $P < 0.01$.

Results

Every month, larval *A. crassus* were found in the swimbladder wall of ruffe. In total, 152 fish (= 66%) were infected with viable L3. Monthly prevalences and mean intensities ranged from 12 to 96% and 1.0 to 5.6 larvae per infected fish, respectively (fig. 1). Statistically significant differences in prevalence (Chi-Square, $P < 0.01$) and mean intensity (Mann-Whitney-U-test, $P < 0.01$) were detected between the warm and cold seasons with higher infection levels during the cold period (fig. 1). The analysis of infection in the different size classes indicated that both fish of the small and large size classes revealed higher prevalences during the cold than the warm season (table 2). Additionally, the prevalence in small fish of the 'winter cohort' was significantly higher than that of large fish of the 'summer cohort' (Chi-Square, $P = 0.01$). Similarly, mean intensities in both size classes were always higher during the cold than the warm season (table 2) and the mean intensity in small fish of the 'winter cohort' was significantly higher than that of large fish of the 'summer cohort' (Mann-Whitney-U-test, $P = 0.001$).

In a single fish, three fourth stage larvae (L4) were detected in the swimbladder wall. Furthermore, during the warm period a small number of dead L3 were also noted in the swimbladder wall.

Discussion

The frequent occurrence of larval *A. crassus* in ruffe from the Oder River suggests that this nematode is widely distributed among the eel population in that locality. Indeed, irregular examinations of eel revealed monthly prevalences between 80 and 100% (Pietrock, unpublished data). A recent helminthological survey carried out in the same habitat on 18 species of fish belonging to seven families (Pietrock *et al.*, 1999a) has shown that other than ruffe, L3 occur occasionally in perch (*Perca fluviatilis*). Given that the infection of eels takes place in particular via paratenic fish hosts (Lehmann *et al.*, 1996), the ruffe thus has to be considered as a major piscine transmitter of larval *A. crassus* and an important source of infections to eels in the Oder River. This, however, does not preclude other aquatic organisms such as snails, amphibians and insect

Table 2. Prevalence and mean intensity of larval *Anguillicola crassus* infection in ruffe (*Gymnocephalus cernuus*) relative to fish size and season.

Size class and season	No. of fish	Prevalence %	Mean intensity (±SD)
8.5–10.5 cm			
Winter	20	80 ^{1,2}	3.3 (1.5) ^{1,2}
Summer	43	53	1.4 (0.9)
11.0–13.0 cm			
Winter	97	81 ¹	4.5 (4.1) ¹
Summer	71	49	1.8 (1.4)

¹Statistically significant differences (Chi-Square (Pearson) and Mann-Whitney-U-test, respectively, $P < 0.05$) compared to fish of the same size class but opposite season.

²Statistically significant differences (Chi-Square (Pearson) and Mann-Whitney-U-test, respectively, $P \leq 0.01$) compared to fish of the opposite size class and season.

larvae which are also known to be potential paratenic hosts (Moravec, 1996; Moravec & Škoriková, 1998).

Infection levels varied throughout the year but were heaviest in ruffe during the cold period. This pattern is in contrast to experimental results where retarded or arrested development as well as increased mortality of *A. crassus* larvae and preadults were observed particularly at cold water temperatures (Petter *et al.*, 1990; Thomas & Ollevier, 1993; Knopf *et al.*, 1998). The course of a parasitic infection, however, depends upon both abiotic and biotic environmental variables. Because the infection of paratenic hosts takes place via the oral uptake of infected copepods, it is conceivable that the detected seasonal periodicity could be caused by a summer decline in the abundance of infected copepods. To date, a wide range of copepods have been shown to act as potential first intermediate hosts (see Moravec, 1994) of which several warm- and eurythermic species occur in the investigation area (Frisch, 1995; Pietrock, 1998). It seems, therefore, unlikely that significant reductions in prevalence and mean intensity of ruffe during summer months are due to insufficient numbers of suitable copepod hosts.

It is, however, possible that the observed pattern of *A. crassus* infection in ruffe from the Oder River is caused by seasonal differences in diet between warm and cold seasons. Such changes in feeding habits of ruffe and consumption of prey in proportion to its abundance have been described elsewhere (Kaalaas, 1995; Kangur & Kangur, 1996). Generally, the primarily benthivorous ruffe is known as a carnivorous species that feeds on all organisms it can catch (Stadel, 1936; Padberg, 1992). During the summer, ruffe encounter a wide variety and high quantity of potential prey organisms, such as fish eggs and larvae, insect larvae and water beetles. Relative to these organisms, small sized copepods may be of minor quantitative importance in the diet during that period and, due to the supposed short life-span of L3 in ruffe (Thomas & Ollevier, 1992a), the infection decreases. In contrast, by the cold period, juvenile prey fish have grown large enough to escape predation by ruffe and numerous insects have emerged from the water (Wesenberg-Lund, 1943). The significant increase in the *A. crassus* infection of ruffe suggests that copepods now probably play a major role in its diet. This hypothesis is supported by the seasonal course of infection with other helminth parasites, such as *Camallanus lacustris* (Nematoda: Camallanidae) and *Proteocephalus cernuae* (Cestoda: Proteocephalidae), both of which use copepods as intermediate hosts and were detected mainly in the cold period (Pietrock, 1998). Seasonal differences in the food choice of ruffe are further supported by the fact that small fish carry heavier infections during the winter than large fish during the summer (table 2). Apparently, ruffe lose their *A. crassus* larvae while feeding and growing during the summer.

To date, more than 30 species of fish have been discovered harbouring infective L3 of *A. crassus* and thus serve as paratenic hosts (Haenen & van Banning, 1990, 1991; Höglund & Thomas, 1992; Thomas & Ollevier, 1992a; Moravec & Konecny, 1994; Székely, 1994, 1995, 1996; Lehmann *et al.*, 1996). Most of those studies, however, are solely faunistic records or results of experimental infections and provide no information on

potential major sources of infection to eels over time. Nevertheless, field data suggest that the ruffe is one of the most important paratenic hosts with prevalences and mean intensities of *A. crassus* ranging from 55.3 to 100% and 2.5 to 39.3 L3 per infected host, respectively (Haenen & van Banning, 1990, 1991; Székely, 1994). Monthly infection levels in ruffe from the Oder River are thus comparable to observations on *G. cernuus* from other European localities. Long-term investigations on *A. crassus* larvae in ruffe and other fishes have been carried out by Thomas & Ollevier (1992a) and Székely (1995). In percid fish, the former authors found higher prevalences and abundances of infection during warm periods and concluded that transmission occurs primarily during the summer. Székely (1995), on the other hand, did not find any clear seasonal fluctuations in the infection of fish. These contradictory results may be explained by differences in the seasonal feeding ecology of the host species or in the seasonal availability of prey. Therefore, the infection of paratenic hosts apparently is not restricted to a particular season. Temporal variations in food web structure and thus prey availability in the study area may influence the host's food preferences and, consequently, may determine the course of infection.

The dynamics of *A. crassus* infections in the final host, the eel has been studied by several authors. In most cases, no clear seasonal differences in occurrence of this parasite were observed (Möller *et al.*, 1991; Thomas & Ollevier, 1992b). This is not surprising as the numerous paratenic hosts thus far discovered may contribute to various degrees to infection of eels. There are occasions, however, whereby a seasonality in the population dynamics of *A. crassus* of eels has been detected (Höglund & Andersson, 1993; Cardoso & Saraiva, 1998). The reasons for seasonal fluctuations in infection patterns may be different at various sampling sites. Amongst others, temperature dependent changes in immunity and/or the feeding rate of hosts may influence the seasonal course of infection. As shown by the present data, however, the availability of infective stages may also differ intraannually and can thus potentially affect the population dynamics of *A. crassus* in the final host.

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References

- Bauer, O.N. (1987) *Key to the parasites of freshwater fish of the USSR*. 584 pp. Leningrad & Nauka (in Russian).

- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W.** (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Cardoso, E.M. & Saraiva, A.M.** (1998) Distribution and seasonal occurrence of *Anguillicola crassus* (Nematoda: Dracunculoidea) in the European eel *Anguilla anguilla* L. from rivers of north Portugal. *Bulletin of the European Association of Fish Pathologists* **18**, 136–139.
- De Charleroy, D., Grisez, L., Thomas, K., Belpaire, C. & Ollevier, F.** (1990) The life cycle of *Anguillicola crassus*. *Diseases of Aquatic Organisms* **8**, 77–84.
- Frisch, D.** (1995) *Artengemeinschaften und Abundanzdynamik cyclopoider Copepoden im Gewässersystem einer Tieflandflu(aue während und nach dem Frühjahrshochwasser (Unteres Odertal, Brandenburg)*. Diploma thesis, 101 pp. Berlin, Free University.
- 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 prey fish to the eel *Anguilla anguilla*. *Aquaculture* **92**, 115–119.
- Hartmann, F.** (1994) *Untersuchungen zur Biologie & Epidemiologie und Schädigung von Anguillicola crassus Kuwahara, Niimi und Itagaki (1974) (Nematoda), einem blutsaugenden Parasiten in der Schwimmblase des europäischen Aales*. 139 pp. Aachen, Verlag Shaker.
- Hirose, H., Sekino, T. & Egusa, S.** (1976) Notes on the egg deposition, larval migration and intermediate host of the nematode *Anguillicola crassa* parasitic in the swimbladder of eels. *Fish Pathology* **11**, 27–31.
- Höglund, J. & Andersson, J.** (1993) Prevalence and abundance of *Anguillicola crassus* in the European eel (*Anguilla anguilla*) at a thermal discharge site on the Swedish coast. *Journal of Applied Ichthyology* **9**, 115–122.
- Höglund, J. & Thomas, K.** (1992) The black goby *Gobius niger* as a potential paratenic host for the parasitic nematode *Anguilla crassus* in a thermal effluent of the Baltic. *Diseases of Aquatic Organisms* **13**, 175–180.
- Kaalaas, S.** (1995) The ecology of ruffe, *Gymnocephalus cernuus* (Pisces: Percidae) introduced to Mildevatn, western Norway. *Environmental Biology of Fish* **42**, 219–232.
- Kangur, K. & Kangur, A.** (1996) Feeding of ruffe (*Gymnocephalus cernuus*) in relation to the abundance of benthic organisms in Lake Vortsjaerv (Estonia). *Annales Zoologici Fennici* **33**, 473–480.
- Knopf, K., Würtz, J., Sures, B. & Taraschewski, H.** (1998) Impact of low water temperature on the development of *Anguillicola crassus* in the final host *Anguilla anguilla*. *Diseases of Aquatic Organisms* **33**, 143–149.
- Kuwahara, A., Niimi, A. & Itagaki, H.** (1974) Studies on a nematode parasitic in the air bladder of the eel. I. Description of *Anguillicola crassa* n. sp. (Philometridea, Anguillicolidae). *Japanese Journal of Parasitology* **33**, 275–279.
- Lehmann, J., Mock, D., Klinger, H. & Kriwet, T.** (1996) Der Kaulbarsch (*Gymnocephalus cernuus*) als vermutlich wichtigste Infektions- bzw. Reinfektionsquelle mit dem Schwimmblasenwurm *Anguillicola crassus* für ältere Aale in Nordrhein-Westfalen. *Fischer and Teichwirt* **11**, 442–445.
- Meinelt, T., Krüger, R., Pietrock, M., Stüber, A., Osten, R. & Steinberg, C.** (1997) Metal load in sediments, pike (*Esox lucius*) and bream (*Abramis brama*) tissues in the River Oder (Germany/Poland). *Archives of Nature Conservation and Landscape Research* **36**, 1–9.
- Möller, H., Holst, S., Lüchtenberg, H. & Petersen, F.** (1991) Infection of eel *Anguilla anguilla* from the River Elbe estuary with two nematodes, *Anguillicola crassus* and *Pseudoterranova decipiens*. *Diseases of Aquatic Organisms* **11**, 193–199.
- Molnár, K., Baska, F., Csaba, G., Glávits, R. & Székely, C.** (1993) Pathological and histopathological studies of the swimbladder of eels *Anguilla anguilla* infected by *Anguillicola crassus* (Nematoda: Dracunculoidea). *Diseases of Aquatic Organisms* **15**, 41–50.
- Moravec, F.** (1992) Spreading of the nematode *Anguillicola crassus* (Dracunculoidea) among eel populations in Europe. *Folia Parasitologica* **39**, 247–248.
- Moravec, F.** (1994) *Parasites of European freshwater fishes*. 473 pp. Prague, Academia.
- Moravec, F.** (1996) Aquatic invertebrates (snails) as new paratenic hosts of *Anguillicola crassus* (Nematoda: Dracunculoidea) and the role of paratenic hosts in the life cycle of this parasite. *Diseases of Aquatic Organisms* **27**, 237–239.
- Moravec, F. & Konecny, R.** (1994) Some new data on the intermediate and paratenic hosts of the nematode *Anguillicola crassus* Kuwahara, Niimi et Itagaki, 1974 (Dracunculoidea), a swimbladder parasite of eels. *Folia Parasitologica* **41**, 65–70.
- Moravec, F. & Škoriková, B.** (1998) Amphibians and larvae of aquatic insects as new paratenic hosts of *Anguillicola crassus* (Nematoda: Dracunculoidea), a swimbladder parasite of eels. *Diseases of Aquatic Organisms* **34**, 217–222.
- 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 Parasitologica* **40**, 39–48.
- Neumann, W.** (1985) Schwimmblasenparasit *Anguillicola* bei Aalen. *Fischer und Teichwirt* **11**, 322.
- Padberg, D.** (1992) *Fischereibiologische Analyse des Kaulbarschbestandes des Großen Müggelsees im Vergleich mit dem der Berliner Havel*. Diploma thesis, 43 pp. Storkow, Ingenieurschule für Binnenfischerei.
- Petter, A.J., Cassone, J. & Le Belle, N.** (1990) Observations sur la biologie des premiers stades larvaires d' *Anguillicola crassus*, nématode parasite d'anguille. *Annales de Parasitologie Humaine et Comparée* **65**, 28–31.
- Pietrock, M.** (1998) *Faunistisch-ökologische Untersuchungen zum Endohelminthenbefall von Zope (Abramis ballerus) und Kaulbarsch (Gymnocephalus cernuus) aus der Unteren Oder*. 228 pp. Berlin, Verlag Wissenschaft und Technik.
- Pietrock, M., Meinelt, T. & Krüger, R.** (1999a) Schadstoffbelastung und Fischgesundheit im Nationalpark 'Unteres Odertal'. pp. 417–430 in Dohle, W., Bornkamm, R. & Weigmann, G. (Eds) *Das Untere Odertal*. Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung (Nägele und Obermiller).

- Pietrock, M., Mattheis, T., Krüger, R. & Meinelt, T.** (1999b) Seasonal dynamics of *Phyllodistomum folium* (von Olfers, 1816) (Trematoda: Gorgoderidae) in blue bream, *Abramis ballerus* (Linnaeus 1758) and ruffe, *Gymnocephalus cernuus* (Linnaeus 1758) from the Oder River (Germany/Poland). *Acta Parasitologica* **44**, 165–169.
- SPSS Inc.** (1999) *Statistical package for the social sciences (SPSS), Version 9.0.1*. Chicago.
- Stadel, O.** (1936) Nahrungsuntersuchungen an Elbfischen. *Zeitschrift für Fischerei* **34**, 45–61.
- Székely, C.** (1994) Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary. *Diseases of Aquatic Organisms* **18**, 11–20.
- Székely, C.** (1995) Dynamics of *Anguillicola crassus* (Nematoda: Dracunculoidea) larval infection in paratenic host fishes of Lake Balaton, Hungary. *Acta Veterinaria Hungarica* **43**, 401–422.
- Székely, C.** (1996) Experimental studies on the infectivity of *Anguillicola crassus* third-stage larvae (Nematoda) from paratenic hosts. *Folia Parasitologica* **43**, 305–311.
- Thomas, K. & Ollevier, F.** (1992a) Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. *Diseases of Aquatic Organisms* **13**, 165–174.
- Thomas, K. & Ollevier, F.** (1992b) Population biology of *Anguillicola crassus* in the final host *Anguilla anguilla*. *Diseases of Aquatic Organisms* **14**, 163–170.
- Thomas, K. & Ollevier, F.** (1993) Hatching, survival, activity and penetration efficiency of second-stage larvae of *Anguillicola crassus* (Nematoda). *Parasitology* **107**, 211–217.
- van Banning, P. & Haenen, O.L.M.** (1990) Effects of the swimbladder nematode *Anguillicola crassus* in wild and farmed eel, *Anguilla anguilla*. pp. 317–330 in Perkins, F.O. & Cheng, T.C. (Eds) *Pathology in marine science*. New York, Academic Press.
- Wesenberg-Lund, C.** (1943) *Biologie der Süßwasserinsekten*. 682 pp. Berlin, Wien, J. Springer Verlag.

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