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Observations on the transmission and the seasonality of infection of the nematode *Raphidascaris acus* in *Salmo trutta fario* in a small trout stream in North Bohemia, Czech Republic

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Summary

Seasonal variations in the occurrence and maturation of the nematode *Raphidascaris acus* (Bloch, 1779) were followed in brown trout, *Salmo trutta fario* L., in the Homolský Brook (the Elbe River basin) at Velké Březno, North Bohemia, the Czech Republic, during the period of 14 months (from April 2000 to May 2001). Gammarids *Gammarus fossarum* Koch were found to serve as the true intermediate host; infective third-stage larvae of *R. acus* 1.35–1.84 mm long were recorded in August and October in a low degree of infection (prevalence 0.006 % and 0.2 %, respectively; intensity 1–3 larvae). Heavy infections with *R. acus* larvae were found in all examined specimens of loach, *Barbatula barbatula* (L.), in which the parasite's third- and fourth-stage larvae occurred mainly in the liver, with the intensity up to about 650 larvae per fish; *B. barbatula* probably serve as both the intermediate and the paratenic host. Small third-stage larvae of *R. acus* were occasionally found encapsulated in the wall of the stomach, pyloric caeca and intestine and in the liver of trout. In this locality, *R. acus* exhibited pronounced seasonal cycles of occurrence and maturation, with the oviposition restricted to a period from May to July; except for one male recorded in September, only larvae occurred in trout from August to April. New infections were acquired by trout all the year round, but mainly from November until April of the next year. The parasite's seasonal maturation cycle was induced by ecological factors, particularly water temperature.

Key words: *Raphidascaris acus*; parasitic nematode; seasonality; maturation; fish; *Salmo trutta fario*; *Barbatula*; *Gammarus*; intermediate host; Czech Republic

Introduction

The nematode *Raphidascaris acus* (Bloch, 1779) is a common and widely distributed parasite of the digestive tract of various predatory fishes in the Holarctic; in Europe, the most frequent definitive hosts are pike (*Esox lucius* L.) and brown trout (*Salmo trutta fario* L.), but it also occurs in other species of salmonids (genera *Acantholingua*, *Hucho*, *Oncorhynchus*, *Salmo*, *Thymallus*) as well as in *Anguilla anguilla* (L.), *Lota lota* (L.), *Perca fluviatilis* L., *Stizostedion lucioperca* (L.) and some other fish species (Moravec, 1994).

The life cycle of this parasite involves obligate intermediate hosts, various species of fish and cyclostomes, and, more rarely, amphibians (Thomas, 1937; Moravec, 1970a, 1994; Supryaga and Mozgovoy, 1974; Smith, 1984; Torres and Alvarez-Pellitero, 1988). Until recently, invertebrates (oligochaetes, crustaceans, chironomids and other aquatic insects) experimentally or naturally infected with *R. acus* larvae were generally considered as preintermediate paratenic hosts of second-stage larvae (Moravec, 1970a, 1994; Smith, 1984; Torres and Alvarez-Pellitero, 1988), because these larvae were always smaller than those undergoing the second moult (Moravec, 1970a) and they currently invaded the liver of fish to attain the third stage, which is only infective to the definitive host. Kosinova and Mozgovoy (1965) and Supryaga and Mozgovoy (1974) allegedly observed the second moult of *R. acus* in all invertebrates studied by them within 2 – 6 days post infection, but this was not confirmed by either the observations of Moravec (1970a) or later studies by Smith (1984) and Torres and Alvarez-Pellitero (1988). However, the recent finding of the third-stage larva of *R. acus* from *G. fossarum* Koch (see Moravec, 1996), morphometrically identical to those from fish intermediate hosts, proved that this invertebrate may serve, in addition to some aquatic vertebrates, as the true intermediate host of *R. acus*. However, it is apparent that most invertebrates play a role as paratenic hosts only.

Seasonal changes of *R. acus* maturation in *E. lucius* were first mentioned by Linstow (1872) in Germany, but more detailed observations were carried out in the populations of pike (*E. lucius*) in Europe (Malakhova, 1961; Supryaga and Mozgovoy, 1974; Moravec, 1979), Central Asia (Engashev, 1964) and North America (Smith, 1986) and in brown trout (*S. trutta fario*) and some other salmonids in Europe (Moravec, 1970a; Žitňan, 1973; Alvarez-Pellitero, 1979). It is apparent from these studies that the maturation cycle of *R. acus* is strictly seasonal, but its pattern may be considerably different in different ecological conditions. The previous observations show that in cooler regions of the temperate zone (Central Europe, Karelia, Canada) *R. acus* occurs only in one generation (Malakhova, 1961; Moravec, 1970b, 1979; Žitňan, 1973; Smith, 1986), whereas it forms two generations a year in warmer regions, as it has been indicated by the data of Engashev (1964) from Central Asia, Supryaga and Mozgovoy (1974) from the Krasnodar District in Russia and Alvarez-Pellitero (1979) in Spain.

In 2000–2001, observations on the life history of *R. acus* under the natural conditions of a small trout stream in North Bohemia, Czech Republic, were carried out, which might enable a more precise determination of factors influencing the circulation of this nematode in the environment. The results obtained are presented herein.

Material and Methods

The study site was the Homolský Brook in Velké Březno, North Bohemia, the Czech Republic; this is a small stream, about 7 km long and 3 – 5 m wide near its mouth, a right tributary of the Elbe River. The fish fauna is represented mainly by brown trout, *Salmo trutta fario* L., in its lower reaches also loach, *Barbatula barbatula* (L.), mud loach, *Misgurnus fossilis* (L.), and chub, *Leuciscus cephalus* (L.), are occasionally found. The population dynamics of *R. acus* was followed in *S. trutta fario* collected by electrofishing in about a 300 m long section of the lower reaches of the stream. Fish samples were taken at regular monthly intervals from April 2000 to May 2001 (see Table 1). Immediately after the transfer of live fish to the laboratory in České Budějovice, these were examined for the presence of helminth parasites. In addition to 179 specimens of brown trout, (*S. trutta fario*), 5 loach (*B. barbatula*) (body length 13 – 16 cm) were examined from this locality. Benthic invertebrates were sampled monthly from April to October 2000 and in May 2001 and these were compressed and examined microscopically for the presence of helminth larvae. The following invertebrates were examined in this way: larvae of aquatic insects: Ephemeroptera 1 002 specimens (*Ephemera danica* 555, *Habroleptoides modesta* 66, *Ecdyonurus dispar* 15, *Ephemerella* 133, *Epeorus* 1, *Heptagenia* 5, Baetidae 137), Plecoptera 15, Trichoptera 125, Diptera 14; Amphipoda (*Gammarus fossarum*): 1 236 specimens; Bivalvia (*Pisidium amnicum*): 171 specimens; Oligochaeta: 12 specimens; Planaria: 4 specimens.

In addition to *R. acus*, the helminth fauna of *S. trutta fario* in this locality includes the monogenean *Gyrodactylus truttae* Gläser, 1974, the trematode *Crepidostomum metoecus* Braun, 1900, the nematode *Cystidicoloides ephemeridarum* (Linstow, 1872) and the leech *Piscicola geometra* (Linnaeus, 1761).

Results

Definitive hosts of R. acus and their food

The brown trout, *S. trutta fario*, was the only definitive host of *R. acus* in this locality. The examinations of trout stomachs revealed that benthic invertebrates (larvae of a variety of aquatic insects, gammarids, oligochaetes and molluscs) formed an important component of trout diet in the course of the whole year, being practically the only food in winter months. However, in the warm period from April to November, a significant proportion of the trout food was formed by terrestrial insects (Hymenoptera, Coleoptera, Hemiptera) and imagoes of aquatic insects and some other terrestrial invertebrates such as spiders, isopods, diplopods and chilopods. Except for July and August, gammarids prevailed in the food. Loach (*B. barbatula*) were found in the stomach of two larger trout specimens.

Occurrence of R. acus in trout

A total of 177 trout were examined (2 additional juvenile specimens with the body length only 3 cm examined in May 2001 were excluded because of their small size; they harboured no parasites) and 113 (64 %) of them were found to be infected with *R. acus* (for survey see Table 1). The prevalence was high in the period from November to May, with the maximum (93 %) in March; decreased values of prevalence were found from June to October, with the minimum (8 %) in August (Fig. 1; Table 1). Similarly, the values of mean intensity were distinctly higher from November to June, as compared to low values in the period from July to October (Fig. 1; Table 1).

The relationship between *R. acus* infection in trout and the size of the trout body was not examined, because the ab-

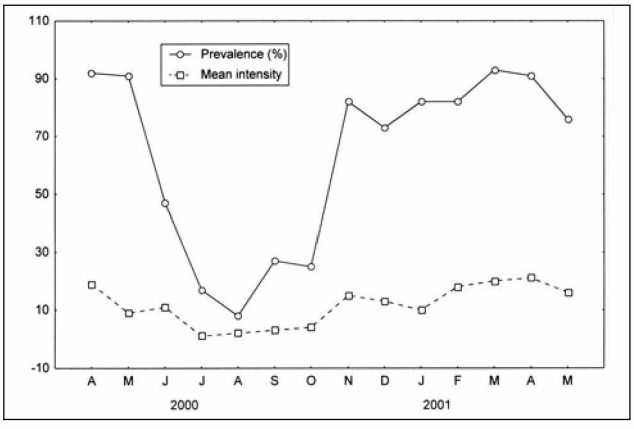

Fig. 1. Seasonal changes in prevalence and mean intensity of *Raphidascaris acus* in *Salmo trutta fario* of the Homolský Brook in the period from April 2000 to May 2001

Table 1. Survey of *Salmo trutta fario* examined from the Homolský Brook and their infection with *Raphidascaris acus*

Year and month	No. of trout examined	No. of trout infected	Prevalence (%)	Abundance	Intensity (mean, range)	No. of nematodes found	Body length of trout in cm (mean, range)
2000							
April	13	12	92	18	19 (1 – 45)	233	17 (15 – 21)
May	11	10	91	8	9 (1 – 24)	87	17 (16 – 21)
June	15	7	47	5	11 (1 – 54)	75	17 (4-25)
July	12	2	17	0.2	1	2	17 (4 – 22)
August	12	1	8	0.2	2	2	20 (15 – 21)
September	11	3	27	0.3	3 (1 – 7)	9	19 (16 – 23)
October	12	3	25	1	4 (1 – 10)	13	19 (14 – 24)
November	11	9	82	13	15 (1 – 90)	138	17 (14 – 21)
December	15	11	73	9	13 (1 – 68)	142	21 (17 – 34)
2001							
January	11	9	82	8	10 (2 – 29)	93	21 (17 – 34)
February	11	9	82	15	18 (2 – 41)	163	22 (14 – 29)
March	15	14	93	18	20 (3 – 55)	276	19 (11 – 22)
April	11	10	91	19	21 (3 – 125)	209	19 (13 – 27)
May	17	13	76	12	16 (1 – 91)	206	19 (15 – 24)
Total	177	113	64	9	15 (1 – 125)	1648	19 (4 – 34)

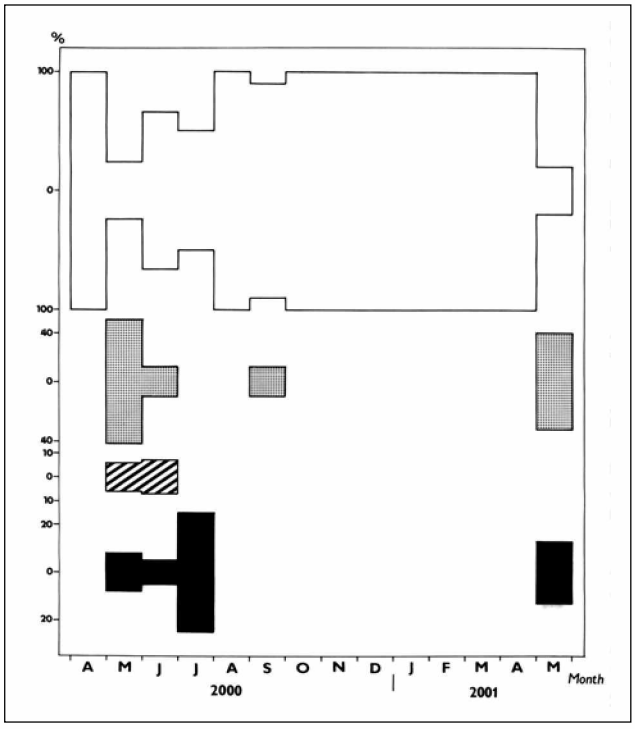

Fig. 2. Monthly changes in the occurrence and state of maturity of *Raphidascaris acus* in *Salmo trutta fario* of the Homolský Brook in the period from April 2000 to May 2001. The data are expressed as percentages of the total number of nematodes found per month: larvae and females without eggs (unsheaded), males (stippled), females containing immature eggs (obliquely hatched), and gravid females containing mature eggs (black)

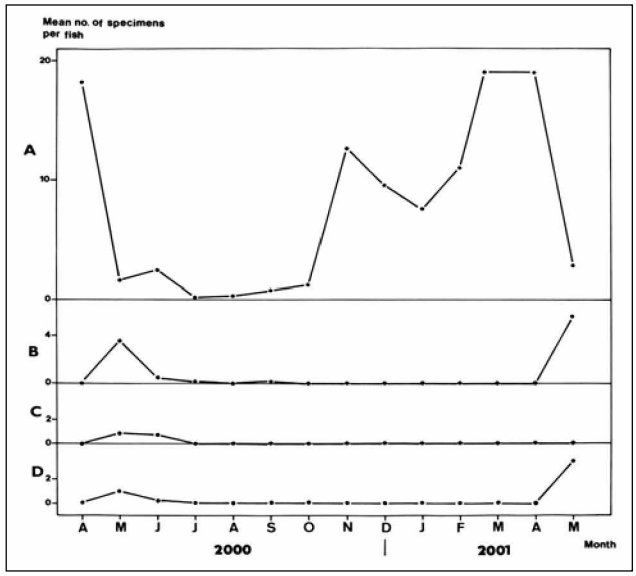

Fig. 3. Monthly changes in mean numbers of specimens of individual stages of *Raphidascaris acus* per trout A – larvae and females without eggs; B – males; C – females with immature eggs; D – females with mature eggs

solute majority of trout specimens examined were of a similar size (15 – 22 cm long) (Fig. 1.). The smallest trout in which *R. acus* infection was recorded measured 11 cm, the largest one 28 cm.

Almost all nematodes were located in the anterior part of the intestine and in the pyloric caeca, occasionally also in the stomach and the posterior part of the intestine.

Seasonal changes in maturation of R. acus

It is evident from Fig. 2 that *R. acus* larvae were present in trout throughout the year, being, except for one male found in September, the only developmental stage of *R. acus* recorded from August to April and prevailing in samples in June and July; their proportion in samples markedly decreased only in May. Fig. 3 shows the quantitative sea-

Table 2. Survey of *Gammarus fossarum* examined from the Homolský Brook and their infection with infective larvae of *Raphidascaris acus*

Year and month	Prevalence (%) (no. infected/ no. examined)	Intensity (mean, range)	Abundance	Total no. of nematodes found
2000				
April	0 (0/220)	0	0	0
May	0 (0/232)	0	0	0
June	0 (0/120)	0	0	0
July	0 (0/118)	0	0	0
August	0.6 (1/168)	1 (1)	0.006	1
September	0 (0/22)	0	0	0
October	0.8 (2/238)	2 (1 – 3)	0.02	4
2001				
May	0 (0/118)	0	0	0
Total	0.2 (3/1236)	2 (1 – 3)	0.004	5

out of the host; a single mature male was found in September. Gravid females with immature eggs were recorded only in May and June, whereas those with mature eggs in the uterus occurred mainly in May, less frequent were in June, and only one specimen was found in July (Figs. 2, 3). The data show that, in this locality, the oviposition of *R. acus* took place only from May to mid-July and that the parasite created only one generation a year.

Intermediate and paratenic hosts of R. acus

Of the examined benthic invertebrates from the Homolský Brook, infective larvae of *R. acus* were found only in the amphipod *G. fossarum*. Of the 1 236 gammarids examined from April to October 2000 and in May 2001, only 3 (0.2 %) were infected, with the intensity 1 – 3 larvae per crustacean; the infected gammarids were collected in August and October (Table 2). The nematode larvae were located free

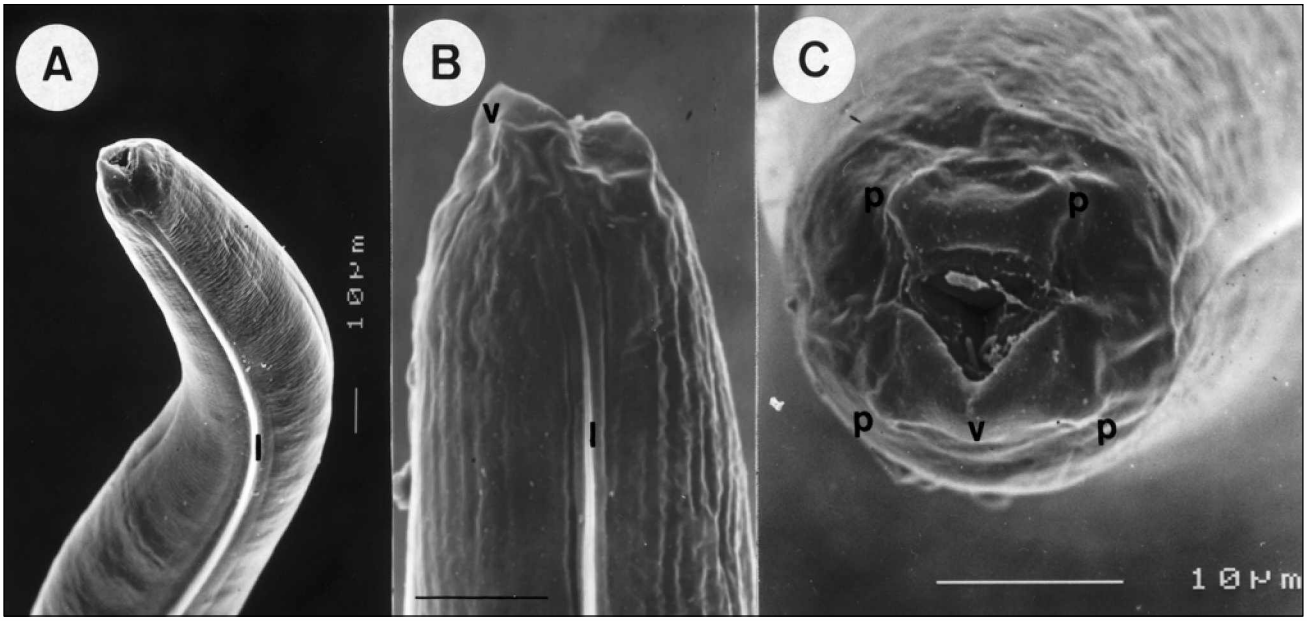

Fig. 4. *Raphidascaris acus* (Bloch, 1779) third-stage larva from *Gammarus fossarum*, SEM micrographs
A – anterior end of body, lateral view; B – cephalic end, lateral view (scale bar = 10 µm); C – cephalic end, apical view. Abbreviations: l – lateral ala; p – cephalic papillae; v – ventral cephalic tooth

sonal changes in the numbers of larvae: it is seen from it that there was a sudden decrease of the absolute numbers of larvae from May to October, with the lowest values in July and August. Whereas in all months except for April the body length of larvae ranged from 1.2 – 8 mm (mostly 3 – 7 mm), the majority of larvae found in May were larger, measuring 10 – 14 mm, although a few smaller larvae about 4 mm long were also present; the larger larvae were at the fourth stage and probably also indistinguishable juvenile females were included. The constant presence of the infective larvae (smaller than 5 mm) indicates that new infections occurred in trout in all months, but mainly from November to April.

Males were present mainly in May and were less numerous in June (Figs. 2, 3), which suggests their gradual passing (not encapsulated) in the haemocoel of the gammarid. The general morphology of these larvae and their measurements showed that they represented the infective third-stage larvae. Consequently, *G. fossarum* can be considered the true intermediate host of *R. acus*.

The larvae of *R. acus* from gammarids measured 1 346 – 1.836 µm in length and 54 – 68 µm in maximum width; cervical alae were 12 µm wide. The ventral cephalic tooth was weakly developed. Oesophagus measured 240 – 297 µm, ventriculus 27 – 33 × 24 – 33 µm; ventricular appendix was 339 – 393 µm long. The distance of the nerve ring and the excretory pore from anterior extremity was 147 – 180 µm and 174 – 210 µm, respectively. The tail was 75 – 87 µm long. The cuticle was smooth; the lips anlages were only feebly developed.

Heavy infections with the third- and fourth-stage larvae of *R. acus* were found in all five examined specimens of the loach *B. barbatula* collected in February, April, August and November. Each fish harboured huge numbers (about 400 – 650) of larvae in the liver, some in the abdominal cavity, and usually a small number of smaller larvae were inside the intestine and the stomach. Larger larvae were mostly encapsulated, usually 1 – 5 larvae per capsule. The liver parenchyma seemed to be badly damaged by these parasites.

Since loach may acquire *R. acus* infection both by swallowing eggs containing second-stage larvae or hatched second-stage larvae along with contaminated food, or by feeding on some preintermediate paratenic hosts (e.g., larval chironomids or aquatic oligochaetes), it is clear that these fish play a role of the obligate intermediate host, in which the nematode larvae attain the stage that is infective to the definitive host. However, larger loach may apparently feed also on the gammarids, intermediate hosts of *R. acus*, which may harbour already infective larvae of the parasite; in this case, loach would serve as paratenic hosts only. But considering the ecology of the loach and a relatively low prevalence of the infective larvae of *R. acus* in gammarids, the role of this fish as a paratenic host of this nematode seems to be negligible.

Besides loach, also trout, *Salmo trutta fario*, was found to serve as the intermediate host of *R. acus* in this locality. In addition to the nematodes found inside the host's digestive tube, small third-stage larvae of *R. acus* inside whitish, globular capsules located in the wall of the stomach, intestine and pyloric caeca (once also in the liver) were occasionally recorded in the period from November until May; each capsule contained a single nematode larva. The total body length of infected fish was 11 – 21 cm. The prevalence of these capsules of *R. acus* in monthly samples ranged between 9 – 18 %, with the intensity of infection 1 – 7 (mean 2) capsules per trout. Because of frequent cannibalism of trout, small trout specimens may become one of the sources of *R. acus* infection for larger trout, whereas the encapsulated *R. acus* larvae in larger trout may represent only a blind alley in the development of this nematode in this locality.

Discussion

In contrast to the earlier assumption that aquatic invertebrates serve as only preintermediate paratenic hosts of *R. acus* (see Moravec, 1970a, 1994; Smith, 1984; Torres & Alvarez-Pellitero, 1988), this paper confirms the recent observation by Moravec (1996) that gammarids may play a role of the true intermediate host of this nematode, in addition to its vertebrate intermediate hosts (fish, amphibians). According to Moravec (1970a), the larvae of *R. acus* undergoing their second moult in their fish intermediate host are 0.74 – 1.05 mm long. However, the larvae from naturally infected *G. fossarum* are approximately twice as long as the largest *R. acus* larvae reported from other invertebrates, and there is no doubt that they are the third-stage larvae, morphologically identical to those from fish intermediate hosts (Moravec, 1970a). Moreover, in the Homolský Brook, *R. acus* third-stage larvae of similar size (1.2 – 2 mm long) were found in the intestine of trout in the samples from September to January, which almost coincides with the records of *R. acus* larvae in gammarids (August, October). Gammarids (only *G. fossarum*) are very abundant in this locality and they form a substantial part of the trout's diet here.

The first record of a gammarid naturally infected with the *R. acus* larva is that of Bradley (1980) from Ireland. He found a single larva in *Gammarus pulex* (out of approximately 50 examined) collected in the Ballinderry River in February 1979; he considered it to be at the third stage, but no morphological or biometrical data were provided. Later, one third-stage larva of *R. acus* 1.77 mm long was found in *G. fossarum* (out of 755 examined) in the Jihlava River, Czech Republic, in April 1992 (Moravec 1996); the common fish in this river was trout.

The present finding of *R. acus* infective larvae in *G. fossarum* indicates that gammarids are common natural intermediate hosts of this parasite. Gammarids (as some other macroinvertebrates) are known to serve as intermediate hosts also for nematodes of the closely related genus *Hysterothylacium* and some other anisakid genera, e.g., *Pseudoterranova*, in which the larval development may occasionally continue up to the fourth stage (Moravec and Nagasawa, 1986).

Although at least 70 fish species are known as the intermediate hosts of *R. acus* (see Moravec, 1994), the highest values of prevalence and mean intensity of *R. acus* larvae in the trout streams of Central Europe are usually recorded in loach, *B. barbatula* (see Moravec, 1970b; Žitňan, 1973); this benthophagous fish is very receptive to *R. acus* infection (Moravec, 1970a), which may result in a considerable mortality in its population (Žitňan, 1967). The heavy infections of *R. acus* in loach are confirmed in the present paper. In contrast to some other European trout streams where other fishes (e.g., *Cottus* spp., *Phoxinus phoxinus*) may be, in view of their availability to the definitive host, a more important source of *R. acus* infection than loach (Moravec, 1970b; Žitňan, 1973), *B. barbatula* is the principle fish intermediate host of *R. acus* (besides young *S. trutta fario*) in the Homolský Brook. This fish acquires the *R. acus* infection by feeding on small benthic invertebrates (e.g., chironomid larvae) serving as preintermediate paratenic hosts of *R. acus* or by swallowing the parasite's free second-stage larvae or eggs containing these larvae along with the food (Moravec, 1994).

It is known that the fish species serving as the definitive hosts may become intermediate hosts of *R. acus* (Moravec, 1994). For example, Alvarez-Pellitero (1979) found young trout (*S. trutta fario*) to be the main intermediate hosts of *R. acus* in the trout streams in northern Spain, whereas older trout were its definitive hosts; the significance of other intermediate host fishes (e.g., *Cobitis calderoni*) in these localities was negligible. In the Homolský Brook, trout were also found to serve as the intermediate hosts of *R.*

acus. However, a relatively low rate of infection was found in middle-sized fish (body length 11 – 21 cm), whereas no fish of smaller size-groups were examined; therefore, it is impossible to estimate the true importance of trout as a sourse of *R. acus* infection for conspecific definitive hosts.

The seasonal dynamics of *R. acus* in the definitive host (pike, trout) has been discussed in more papers; it is clear from them that the values of *R. acus* prevalence and mean intensity are considerably variable and may differ according to the characters of a locality, being influenced by many factors (Moravec, 1994). Observations on the seasonal dynamics of *R. acus* in trout and pike in the Czech Republic (Moravec, 1970b, 1979) make it possible to state only that while there was a relatively high infestation of the definitive hosts from autumn to spring, the values of *R. acus* prevalence and mean intensity suddenly decreased in summer, being sometimes even zero in some summer months. The same was found in trout of the Homolský Brook. Apparently, these changes are closely related with the seasonality in *R. acus* maturation.

Observations in the Homolský Brook confirmed the strictly seasonal maturation cycle of *R. acus* in this locality and made it possible to determine the nature of its life history and population dynamics within the study area throught the year. The egg-producing females were present only from May until June, exceptionally to mid-July. After the oviposition, there was a period in summer (July, August) when these nematodes (including larvae) were almost absent from trout, this being apparently associated not only with the disappearance of nematodes of the old generation from the host but also with the increased water temperatures that in some intestinal fish helminths result in their elimination from the host's body (Kennedy, 1967; Cannon, 1972; and others). Even though the principal factor causing the seasonality in *R. acus* seems to be the water temperature, there are other factors influencing this process, for example the fact that trout feed almost exclusively on terrestrial insects during the summer.

Trout acquire the *R. acus* infection by feeding on intermediate hosts (gammarids, loach, small trout) harbouring infective third- and fourth-stage larvae of the nematode. New infections are acquired by trout throughout the year, but mainly from November until April of the next year. The larvae start to grow substantially in April (most of them are already 10 – 14 mm long), but there is a quick development from larvae to adults only in May; a single male recorded in September may show that, quite exceptionally, some larvae may attain maturity in autumn. The above data show that *R. acus* in trout of the Homolský Brook forms only one generation a year.

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