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ON THE LIFE HISTORY OF THE NEMATODE CYSTIDICOLOIDES TENUISSIMA (ZEDER, 1800) IN THE RIVER BYSTŘICE, CZECHOSLOVAKIA

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Abstract. The life history of the nematode *Cystidicoloides tenuissima* was followed from April 1967 until July 1968 in the natural environment of the River Bystřice. The incidence, intensity of infection, and also the maturation of the nematode in the definitive host (*Salmo trutta* m. *fario*) indicate that the parasite has two generations a year in the locality under consideration — a spring generation and a less numerous autumn generation. The egg-producing female nematodes are present only from May until July, and from September until October. This seasonal rhythm is largely due to a seasonal occurrence of the intermediate hosts and to the water temperature, although the effects of other factors cannot be excluded. In the River Bystřice the mayfly nymphs, *Habroleptoides modesta* and *Ephemera* sp., were found to act as the intermediate hosts of *C. tenuissima*.

Cystidicoloides tenuissima (Zeder, 1800) is a frequent parasite of the stomach of salmonid fishes (less often of other fishes) of Europe, Asia and North America. According to Choquette (1955) the intermediate hosts of this species in Canada are the larvae of *Hexagenia recurvata* and *Polymitarcis* sp. (*Ephemeroptera*); in Europe and Asia, the natural intermediate hosts of this nematode have not been recorded as yet. Experimental infections performed by Moravec (1971) during his studies on the life history of *C. tenuissima* revealed that the larvae of this species might develop in the mayfly nymphs *Habrophlebia lauta*, *Habroleptoides modesta* and *Ephemera danica*. The reservoir hosts are not known; the definitive hosts (fishes) are infected by feeding on mayfly nymphs harbouring the invasive larvae of *C. tenuissima*.

The development, population dynamics and maturation of two of the most common parasitic nematodes of the brown trout in Czechoslovakia — *Cystidicoloides tenuissima* and *Raphidascaris acus* — were followed from April 1967 until July 1968 in the River Bystřice (a tributary of the River Morava). The characteristics of the River Bystřice and its fish fauna were described in an earlier paper (Moravec 1970), concerned with the species *R. acus*.

MATERIALS AND METHODS

The population dynamics and maturation of *C. tenuissima* were followed in the host *Salmo trutta* m. *fario* from the trout zone of the River Bystřice, in the vicinity of the village Hrubá Voda. Samples of fish were taken at regular monthly intervals (using an electric fishing machine) together with regular samples of the benthic invertebrates. From this locality a total of 209 brown trout, *Salmo trutta* m. *fario* L., 7 grayling, *Thymallus thymallus* (L.), 10 bullhead, *Cottus gobio* L., and 21

Siberian sculpin, *Cottus poecilopus* Heck., were examined. A survey of the brown trout examined in the individual months and the degree of infection with *C. tenuissima* is given in Table 1; a survey of the invertebrates examined is given in an earlier paper (Moravec 1970).

OBSERVATIONS

1. The definitive host of *C. tenuissima* and its food

The following fish species, inhabiting the River Bystřice, may be utilized as potential definitive hosts of *C. tenuissima: Salmo trutta* m. *fario, S. gairdneri, Hucho hucho* and *Thymallus thymallus*. Since the species *S. gairdneri* and *H. hucho* are very rare in the

Table 1. The seasonal variation in the degree of infection of the brown trout by *C. tenuissima* in the vicinity of Hrubá Voda

Month and year	No. of trout examined	No. of trout infected	Incidence %	Intensity of infection	Mean intensity of infection
1966					
June	13	13	100	4 to 51	20 to 21
1967					
April	11	11	100	8 to 98	41 to 42
June	23	22	95.6	1 to 92	38 to 39
July	13	13	100	2 to 93	34
August	30	18	60	1 to 85	14 to 15
September	16	14	87.5	1 to 28	11
October	10	10	100	2 to 94	29
November	6	6	100	4 to 32	10 to 11
December	10	10	100	2 to 42	12 to 13
1968					
January	6	6	100	8 to 94	44 to 45
February	14	14	100	6 to 51	27 to 28
March	11	11	100	8 to 51	25 to 26
April	22	22	100	8 to 134	38 to 39
May	13	13	100	3 to 111	50 to 51
July	11	11	100	2 to 83	19 to 20

River Bystřice, they have not been examined helminthologically as yet. Also *T. thymallus* is relatively rare in this river. Of a total of 7 *T. thymallus* examined in different months (May, June, July, August and December), these nematodes were found in only two of them, the intensity of infection being very low (one and four nematodes per fish). This indicates that in the locality in question the grayling is considerably less attacked by *C. tenuissima* than the brown trout; consequently the main definitive host is the brown trout (*S. trutta* m. *fario*). Also three juveniles of *C. tenuissima* were found in the gall bladder of one specimen of *Cottus gobio* in this locality. The finding of juveniles in an atypical organ supports the supposition that the bullhead is not one of the normally utilized definitive hosts of this nematode.

Since the composition of the helminth fauna is considerably affected by the diet of the host, the character of the food of the brown trout was also recorded monthly. As a result of this survey it became obvious that from April—May until August the food of the brown trout was largely composed of all kinds of terrestrial insects and winged imagoes of aquatic insects; larvae of aquatic insects and small crayfish were taken less

frequently. Bullhead and Siberian sculpin were totally absent from the diet of the brown trout at that time. Their diet from September until April—May was composed entirely of available aquatic insect larvae, and fish of the genus *Cottus*.

2. Intermediate hosts of *C. tenuissima*

According to Choquette (1955) and Moravec (1971) there is only one intermediate host involved in the life history of the nematode *C. tenuissima*, i.e. various mayfly species. In the regular monthly samples of benthic invertebrates, taken in the vicinity of Hrubá Voda, invasive larvae of *C. tenuissima* were found in mayfly nymphs of the species *Habroleptoides modesta* and *Ephemera* sp. only in the period from November until April. However, the incidence and intensity of infection were considerably different in these two intermediate hosts. While the incidence of larvae in *H. modesta* was 1.74 % of the total of larvae examined (1.03—4.48 % in the individual samples) and the intensity of infection was 1—2 larvae per host, these values were considerably higher in *Ephemera* sp. The total incidence was 40 % (14.28—75 % in the individual samples), the intensity of infection 1—4 larvae per mayfly. The higher degree of infestation of *Ephemera* sp. as compared with that of *H. modesta* appears to be connected with the different living conditions of the nymphs of both these species. While the nymphs of *H. modesta* live under stones and under fallen leaves and can thus be infected with the eggs of *C. tenuissima* settling there, the nymphs of *Ephemera* sp. live mostly in shallow water in the thick layer of detritus through which these nymphs bore their passages. There, the settlement and concentration of eggs of *C. tenuissima* seem to be much higher than in the other parts of the river and this may account for the higher infestation of *Ephemera* sp. In spite of that, *H. modesta* has to be considered as the chief intermediate host in this locality, being the most numerous mayfly species there; the occurrence of *Ephemera* sp. is considerably lower. Although we succeeded in experimental infection of *Habrophlebia lauta* with *C. tenuissima* (Moravec 1971), we did not find these to be intermediate hosts under field conditions; but this may have been due to the fact that we examined only an inadequate number of individuals.

3. Seasonal changes in incidence and mean intensity of infection and maturation of *C. tenuissima* in the brown trout

The monthly incidence of infection and mean intensity values in *S. trutta* m. *fario* are given in Fig. 1. The only remarkable decrease in the incidence of infection occurs in August and September. During the remaining months, the incidence is constantly high, being mostly 100 %. However, while the incidence shows only one marked variation, there are three remarkable decreases in the mean intensity, the first being in August and at the beginning of September (concomitant with the decrease in incidence), the second in November and December and the third during February and March.

In the locality under consideration, *C. tenuissima* has two generations a year. This finding has been derived from the fact that females containing eggs, which are capable of infection the intermediate hosts, are present only from May until July and again from September until October.

DISCUSSION

On the basis of the present observation it is possible to determine the nature of the life history and population dynamics of *C. tenuissima* in the brown trout within the sampling area near Hrubá Voda throughout the year. In this locality *C. tenuissima* has two generations — a spring generation and a slightly weaker autumn generation. The females

of the spring generation produce mature eggs (containing first-stage larvae) from May to July. These eggs released into the water along with the host's faeces, are carried by the river either to the calm backwaters or become lodged among plant remains under the stones near the river banks. The backwaters are largely populated by mayfly nymphs of the genus *Ephemera* boring their passages through the detritus, while the mayfly nymphs of the family *Leptophlebidae* (mainly the species *Habroleptoides modesta*) live in plant remains under stones at the river banks, where the current is slow. The eggs are eaten by the nymphs together with the detritus; first-stage larvae hatch inside the

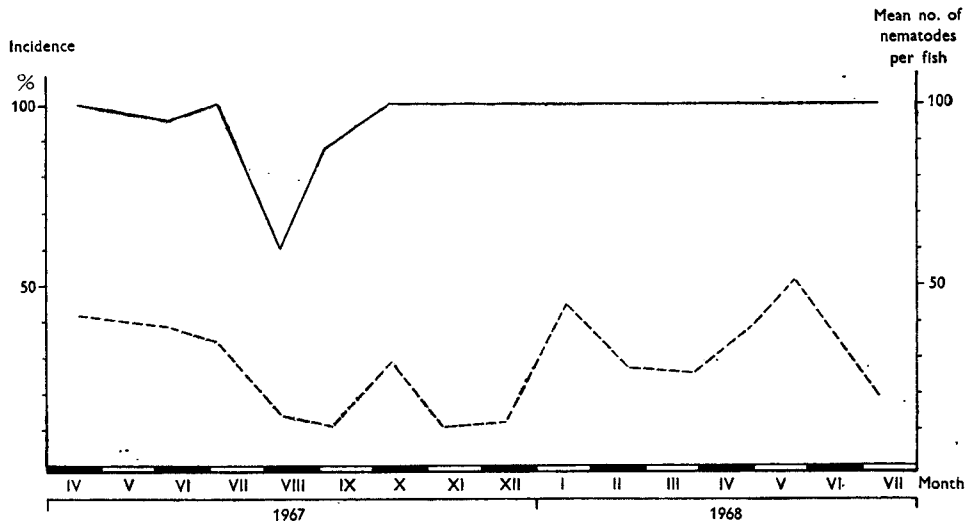

Fig. 1. Monthly changes in the incidence (————) and mean intensity (— — — —) of infection of the brown trout by *C. tenuissima* in the River Bystřice near Hrubá Voda.

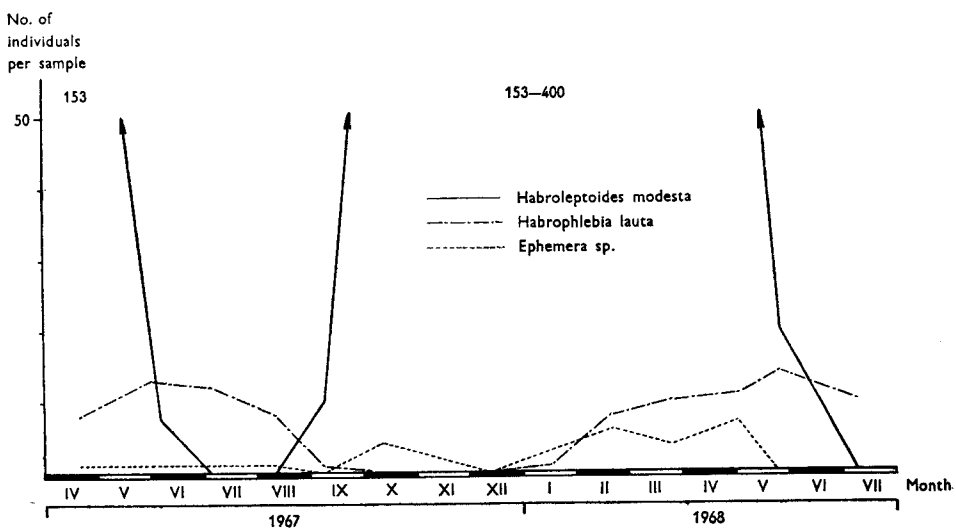

Fig. 2. Monthly changes in the representation of the main intermediate hosts of *C. tenuissima* in benthic samples collected in the River Bystřice near Hrubá Voda.

body of this intermediate host, reaching the infective stage approximately within one month. Since, in the spring, the eggs of *C. tenuissima* are laid at about the same time as the mayfly *Habroleptoides modesta* completes its metamorphosis, this results in a considerable decrease and, finally, a complete disappearance of sufficiently large nymphs which may be available for infection. Therefore, the intermediate hosts utilized in the summer months (July to August) are, apparently, only the larvae of *Ephemera* sp. and possibly larvae of *Habrophlebia lauta*, but the occurrence of both these species is considerably lower than that of *Habroleptoides modesta*. Consequently, a remarkable decrease of incidence and intensity of infection occurs in the brown trout during August and September (Fig. 1); this is supported by the fact that at this time the brown trout feed mainly on terrestrial insects, aquatic insects representing only a small part of their diet. When the last nematodes of the spring generation have left the fish during the first half of July, only the juveniles of *C. tenuissima* remain in the digestive tract of the brown trout. These develop relatively quickly and the adult females of the autumn generation produce eggs during September and October. The relatively fast development of *C. tenuissima* both in its intermediate and definitive host seems to be connected with the temperature of the water and, in the definitive host, perhaps also with the more intense uptake of food by the brown trout. By the time, the adult females of the autumn generation of *C. tenuissima* start egg-production, the numbers of large nymphs of *H. modesta* (Fig. 2) have again become big enough to be utilized as the main intermediate host of *C. tenuissima*. By the end of October, the last nematodes of the autumn generation leave the digestive tract of the brown trout, and only juvenile forms are found in the winter months; these develop only very slowly under the influence of the low water temperature. During November and December, the stomach of the brown trout harbours only larvae of *C. tenuissima*; in January and February also male and young female nematodes without eggs are present. In the spring months, from March until April, when the water temperature has increased, the digestive tract of the brown trout contains already females with immature eggs. Egg-production starts in May and continues until the first half of July.

The brown trout is continuously infected during the winter and spring period. This is also supported by the fact that, during this time, the brown trout feeds mainly on the larvae of aquatic insects (see p. XX). While the incidence of infection in the brown trout is constantly 100 % during the winter and spring months, the increase of the mean intensity of infection is not constant during this time, but shows a twice as rapid decline (Fig. 1). The first decline occurs in November and December and is partly connected with the disappearance of the nematodes of the autumn generation from the brown trout during October, partly with the spawning period of the brown trout which in this locality begins in November and continues until January. As shown in the literature (Dyk, Podubský, Štědronský 1949), feeding of the brown trout during its spawning period is substantially reduced or suspended completely. This host's fast may result in the gradual departure of some of the nematodes from the digestive tract. The second decline of the mean intensity of infection (Fig. 1) at the end of February and in March can be explained by the cessation of feeding during the spring flood. Similar two declines in the mean intensity of infection (only slightly lagging behind in time) were observed also in nematodes of the species *Raphidascaris acus* in the brown trout from the same locality (Moravec 1970).

The sources of infection of the brown trout are not only the nymphs but also the imagoes and subimagoes of the mayflies as confirmed in experiments by Moravec (1971). The nature of the brown trout's diet in the various months of the year suggests that, in the spring and the summer, the brown trout acquire infection most frequently from the mayfly imagoes because, during these months, they feed largely on

all kinds of terrestrial insects and adult aquatic insects; the larvae of aquatic insects represent only a small part of their diet.

The seasonal rhythm in population dynamics and maturation of parasitic worms has often been recorded and again confirmed by the results of our observation of *C. tenuissima* in the River Bystřice. In species with a seasonal maturation, this occurs always in spring and continues sometimes into early summer, while worms with two generations a year mature always in spring and in autumn. This similarity in seasonal periodicity in various fish helminths has led many workers to believe that there is a common causal factor, water temperature. Some authors also considered variations in host feeding habits, seasonal variations in the availability of invasive larvae, and changes in the physiological resistance of the host to infection (see Kennedy 1968).

It appears that the factors responsible for the seasonal periodicity in the maturation of *C. tenuissima* are the seasonal occurrence of the intermediate hosts and water temperature. The influence of water temperature on the duration of the life cycle of nematodes of the order *Spirurida* has been repeatedly confirmed. For example if the temperature of water is decreased by 10 °C, development of the fish nematode *Camallanus lacustris* lasts twice as long as that under the laboratory temperature (Kupryanova 1954). In low temperatures the development may even become arrested. In fish parasites, however, the temperature of the surrounding water does not influence only the length of development in the intermediate host, but also that in the definitive host, because the body temperature of the host depends to some degree on the temperature of the surrounding water. In *C. tenuissima*, this dependence of the length of development on the water temperature is very marked; in summer, the development of the next generation lasts only 2 months, while the spring generation needs as long as 8 months. Also seasonal variation in the resistance of the host to infection or of its hormones may participate in the seasonal periodicity of *C. tenuissima*; unfortunately none of these factors has been followed as yet. Fasting or seasonal changes in the host's choice of food seem to influence only the incidence and intensity of infection, but not the rhythm of maturation.

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