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THE ECOLOGY OF CREPIDOSTOMUM SPECIES (ALLOCREADIIDAE: DIGENEA) IN THE SALMONOIDS OF LAKE YLI-KITKA IN NORTHEASTERN FINLAND

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Abstract. *Crepidostomum* spp. were studied from 417 whitefish (*Coregonus acronius* Rapp, 1854), 220 vendace (*Coregonus albula* L.) and 38 brown trout (*Salmo trutta* m. *lacustris* (L.)) from Lake Yli-Kitka in northeastern Finland during 1980—1983.12.7 % of the whitefish were infected with *Crepidostomum* with a mean intensity of 4.6 worms per infected fish. The species involvedare *C. farionis* (Müller, 1784) and *Crepidostomum wikgreni* Gibson et Valtonen, 1988, which differed from *C. farionis* in the number and size of the eggs. Both types were encountered in the gall-bladder and intestine, but were unable to be distinguished as immature stages. 21 % of the brown trout harboured *C. farionis* in the intestine with a mean number of 1.5 worms per infected fish. Two *C. farionis* specimens occurred also in the intestine of one vendace. Whitefish smaller than 150 mm did not harbour *Crepidostomum* specimens, but in bigger fish the prevalence and the mean intensity of infection increased to a certain limit as the fish got larger. The prevalence of *Crepidostomum* infection also clearly increased during the three seasons in the three size-groups studied. The seasonal pattern of *Crepidostomum* in whitefish of the size ≧ 150 mm was variable in that the lowest values, both in the prevalence and mean intensity of infection, occurred between September and December in 1980 and between April and August in 1982. Reinvasion was found throughout the year, although the main recruitment occurred during autumn and early winter. Eggs matured between late spring and early autumn. The smallest worms occurred mainly in the gall-bladder, and most of the gravid specimens were located in the intestine. Both the variance-to-mean ratio and the low values of the parameter k of the fitted negative binomial distribution reveal the *Crepidostomum* specimens are overdispersed in the whitefish of Lake Yli-Kitka.

Crepidostomum farionis (Müller, 1784) is a circumpolar trematode species and has been found commonly in the intestine and more seldom in the gall-bladder of salmonoid fishes. It has been reported previously in Finland by Jääskeläinen (1911, 1913a, b), Hakala et al. (1981), Gibson and Valtonen (1988), but was not found in fish of the Bothnian Bay by Valtonen et al. (1984). *C. wikgreni* is a new species described by Gibson and Valtonen (1988). It is morphologically similar to *C. farionis* but is distinguished by its unusually large eggs (Gibson and Valtonen 1988). Other papers from the fish of Lake Yli-Kitka include those on acanthocephalans (Valtonen et al. 1981), *Azygia* spp. (Gibson and Valtonen 1981), *Triaenophorus* spp. (Valtonen et al. 1984), *Bunodera luciopercae* (Rahkonen et al. 1984), *Phyllodistomum umblae* (Rahkonen and Valtonen 1987) and proteocephalids (Valtonen and Rintamäki 1989, Rintamäki and Valtonen 1989).

The ecology of *Crepidostomum* spp. in coregonids is poorly known. Information about the seasonal occurrence and the infection in relation to host age and size of *C. farionis*, and/or the related *C. metoecus* (Braun, 1900) is available from *Coregonus* spp. (Watson and Dick 1979) and *Salmo* spp. (see e.g. Thomas 1957, 1958, Awachie and Chubb 1964, Awachie 1968, Hare and Burt 1975, Bwathondi 1976, Moravec 1982, Mariaux 1986).

The present work will shed some light on the occurrence of *Crepidostomum* in the fish of a large northern Finnish lake, which has been isolated from the rest of the Finnish water bodies for 8400 years (Heikkinen and Kurimo 1977). The results include seasonal patterns, parasite burden in relation to host age and size and the frequency distributions in whitefish (*Coregonus acronius* Rapp, 1854).

MATERIALS AND METHODS

Lake Yli-Kitka is a part of a large lake complex called Suur-Kitka, the total area of which is about 295 km². It is located in northeastern Finland (GRID 27 °E 734:58), 240 m above sea level (Fig. 1). The waters of the lake flow to the White Sea via the River Kitkajoki. Lake Yli-Kitka is oligotrophic and the only large lake in northern Finland in a natural state (Myllymaa 1978), and it is associated with the International Project Aqua. Ice covers the lake for about seven to eight months of the year from October to the end of May. The water is warmest at the end of July or the beginning of August when it may reach 18 °C. The water temperature was below 10 °C between the middle of September and the end of June in 1981 and 1982 (Kankaala et al. 1984).

Crepidostomum specimens were examined from 417 whitefish (*Coregonus acronius* Rapp, 1854), 220 vendace (*Coregonus albula* L.) and 38 brown trout (*Salmo trutta* m. *lacustris* (L.)). Monthly random samples of about 20 whitefish and vendace were caught using seine nets. Brown trout were caught by gill-nets. Due to the seasonal migrations of the fish, samples had to be obtained from four areas of the lake. Most of the fish were, however, caught at sites A and D (Fig. 1).

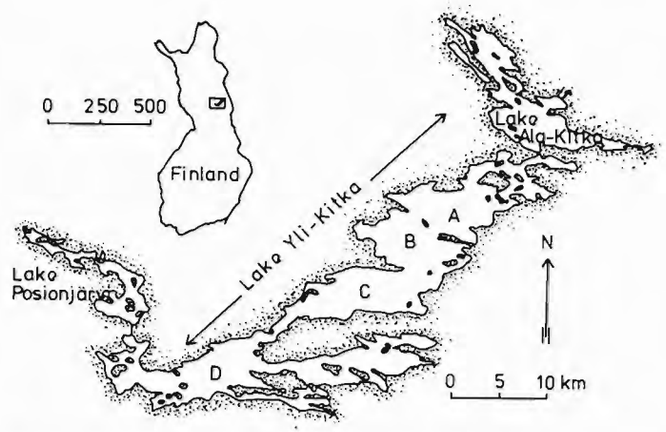

Fig. 1. Location of Lake Yli-Kitka and the study areas.

The question of coregonid taxonomy has been on object of speculation during last years in Scandinavia. Using gill-raker distribution, spawning behaviour and geographical location it was stated by Kallio—Nyberg and Koljonen (1988) that *C. acronius* Rapp, 1854, as suggested by Svärdson (1979), is the correct name for the present whitefish species. In the paper of Rahkonen and Valtonen (1987) the whitefish species was reported as *Coregonus* sp.

The vendace of Lake Yli-Kitka are known for their very small size as compared to vendace in other Finnish lakes, e.g. in the neighbouring Lake Ala-Kitka (Fig. 1) where the mean length of vendace in catches in 1981 was 145 mm (Hyytinen 1985) as compared to only 97 mm in the present material. In Hyytinen's material the samples were collected throughout the year using seine nets as in the present case.

Live trematodes recovered from the intestine and gall-bladder were fixed during the early part of the project in formalin, but later in glacial acetic acid and preserved in 70 % ethanol. Some of the specimens were stained in Mayer's paracarmine and mounted in Canada balsam for identification, which was done by Dr. D. I. Gibson (British Museum (Natural History)). Worms from frozen fish were placed directly in 70% ethanol. They were divided into two categories, immature and ovigerous worms.

The dispersion of *Crepidostomum* in relation to fish length and seasonality in fish of a length ≧ 175 mm was studied using variance-to-mean ratios. When overdispersed (variance > mean) a negative binomial distribution was fitted to the frequency distributions. The maximum likelihood method was used to estimate parameter k of the negative binomials (Bliss and Fisher 1953). The χ^2 test was used to assess the accuracy of the fit.

RESULTS

1. Occurrence of *Crepidostomum* spp. in the fish of Lake Yli-Kitka

Crepidostomum specimens were found in 12.7 % of the whitefish, the mean intensity per infected fish being 4.6 worms. Among *C. farionis* other *Crepidostomum* specimens were found which differed from *C. farionis* in the number and size of eggs. This second form was referred to as *Crepidostomum* sp. (Hakala et al. 1981) and it was found initially only in the gall-bladder. Further studies carried out by Gibson and Valtonen (1988) confirmed that the specimens represented a new species, *C. wikgreni*, which was found both in the gall-bladder and intestine of whitefish. Unfortunately immature specimens of this species and *C. farionis* appear to be indistinguishable. Only the ovigerous worms which occurred mostly during a short time between late May and June were suitable for species identification. This is why in the present paper the two species are handled together. Of the identified ovigerous material during 1980—1986 64 % were *C. wikgreni* and 36 % *C. farionis*. Specimens of the two *Crepidostomum* species were encountered both in the intestine and gall-bladder of the whitefish, where no other trematodes were found. Both the prevalence and mean intensity of infection were higher in the gall-bladder compared to that found in the intestine. 21.1 % of the brown trout were infected with *C. farionis* only. All worms were found in the intestine with the mean intensity of 1.5 worms per infected fish. In addition, two specimens of *C. farionis* were found in the intestine of a vendace (Table 1).

Table 1. Occurrence of *Crepidostomum* spp. in the whitefish and *C. farionis* in the vendance and brown trout of lake Yli-Kitka

	Site	Date	No. of fish	Prevalence %	$\bar{x}$ (inf. fish ± S. E.)	Range
Coregonus acronius	Gall-bladder	III 80—VI 81, III—X 82	417	9.1	5.5 (1.2)	1—29
	Intestine	III 80–VI 81, III–X 82	417	4.6	1.8 (0.4)	1—6
	Together	III 80–VI 81, III–X 82	417	12.7	4.6 (0.7)	1—29
C. albula	Intestine	III 80—IV 81	220	0.5	2.0 (0.0)	2—2
S. trutta m. lacustris	Intestine	XI 80, I—XII 81, I—IV 82, I—XI 83	38	21.1	1.5 (0.3)	1—3

2. *Crepidostomum* infections in relation to the length and age of whitefish

Fish smaller than 150 mm did not harbour *Crepidostomum* specimens. The proportion of whitefish infected with *Crepidostomum* increased up to the length group of 215—224 mm, but in the case of the largest fish (size class ≧ 225 mm) it decreased slightly. The mean intensity of infection also increased as the fish got larger, but a level of 1—3 worms per infected whitefish appeared to predominate in all the length groups except that of 185—194 mm (Fig. 2). When handling the prevalence of *Crepidostomum* infection according to the age of whitefish, a clear increase was found from 0 % in one year old fish up to nearly 40 % in fish of five years or older. The prevalence of infection was 10.5 % at two years, 12.4 % at three years and 17.6 % in four year old fish. The mean intensity of infection increased up to the age of four years (1 year =

0, 2 years = 3.0, 3 years = 3.0, 4 years = 6.2, 5 years = 3.5). The mean number of worms per fish and the overdispersion index ($s^2/\bar{x}$) also tend to increase with fish length up to 214 mm, indicating a progressively more pronounced overdispersion with increasing fish length. Nevertheless, in the two largest size-classes the variance-to-mean ratio decreased (Fig. 3). Fig. 4 indicates that the prevalence of infection also clearly increased during the three seasons studied.

Only brown trout with predatory habits (size of 380—510 mm) were infected with *Crepidostomum farionis*.

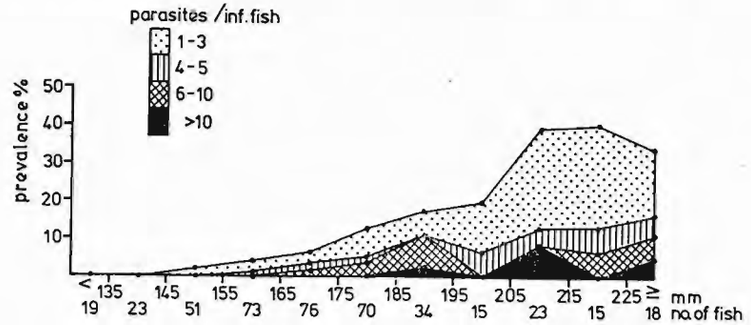

Fig. 2. Occurrence of *Crepidostomum* spp. in relation to the length of whitefish from Lake Yli-Kitka during 1980—1982.

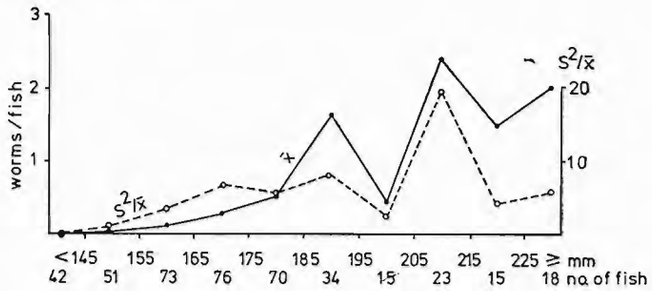

Fig. 3. Worms per fish and variance-to-mean ratio of *Crepidostomum* spp. in whitefish in relation to host-size in Lake Yli-Kitka during 1980—1982.

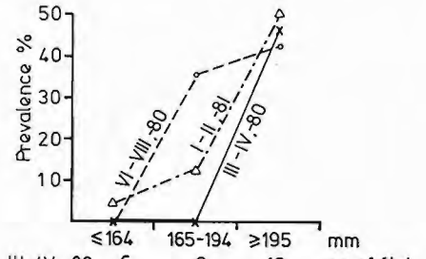

Fig. 4. Prevalence of *Crepidostomum* spp. in three size-classes of whitefish from Lake Yli-Kitka in three seasons during 1980—1981.

3. Seasonal occurrence of *Crepidostomum* spp. in the whitefish of size ≧ 150 mm

The seasonal variation of *Crepidostomum* spp. infection in fish of the size ≧ 150 is shown in Fig. 5, where the proportions of the worms in the intestine and gall-bladder is depicted. *Crepidostomum* specimens were found in the gall-bladder throughout the year, but in the intestine only between April and September except for one worm in January 1981 (Fig. 5).

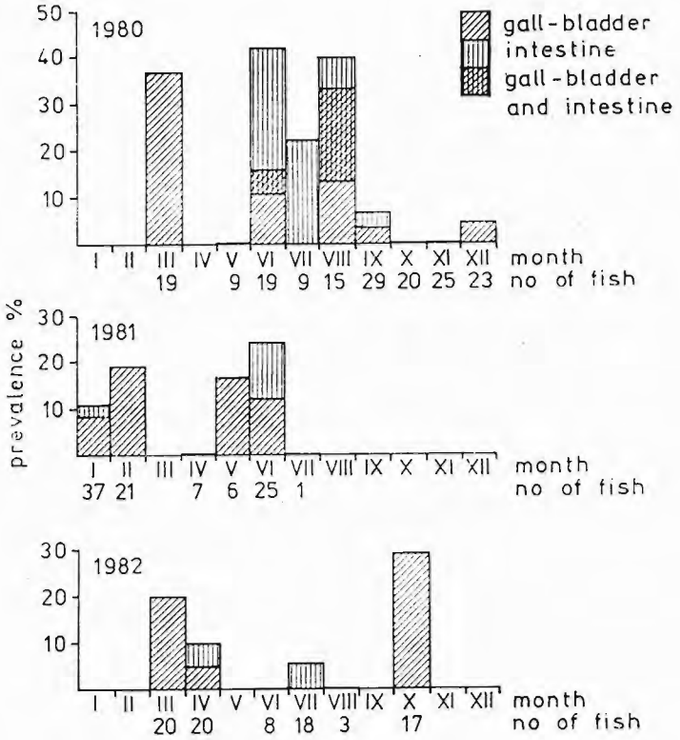

Fig. 5. Prevalence of *Crepidostomum* spp. and the proportions of worms in the gall-bladder and intestine in monthly samples of whitefish (≧ 150 mm) from Lake Yli-Kitka during 1980—1982.

A clear pattern emerged in the seasonal variation of the prevalence of infection with the lowest values in May and September-December, 1980. In 1981 no fish were studied during the last half of the year and in 1982 the loss of parasites occurred much earlier, i.e. in June and August no worms were found, although in these samples the proportion of small fish (< 150 mm) was great and since the sample size used in the seasonal study was small. Nevertheless, it seems that in Lake Yli-Kitka the seasonal pattern of *Crepidostomum* in whitefish is quite flexible and may vary in different years. In each of the three years and in each site studied, the intensity of infection followed the same pattern as the prevalence.

Analysis of the seasonal occurrence of developmental stages of *Crepidostomum* during the different years studied indicates that immature worms (length 0.4—2.0 mm)

occurred in the whitefish throughout the year. Very small (< 1 mm) specimens were encountered in the autumn (August-December) and also in March and June of 1980 and in April of 1982. Immature trematodes were located in the gall-bladder in most cases. In the intestine immature specimens were found mostly during the period June-September, the smallest worms being found in August and September 1980.

Ovigerous worms (1.3—2.8 mm) were encountered mainly from May until the end of August and most of them were located in the intestine. In addition to some mature worms in the gall-bladder in May-June, a single mature worm was found in January and February of 1981. The length of the worms also followed a clear seasonal pattern: worms were longest in May-July ($\bar{x}$ 1.7 $\pm$ 0.1 mm, n = 50) and shortest in August-December ($\bar{x}$ 0.9 $\pm$ 0.1 mm, n = 31).

C. farionis specimens were found in the intestine of brown trout in November 1981, February 1982, February and March 1983 and in the intestine of vendace in August 1980, and all of them were ovigerous.

4. Dispersion and frequency distributions

The overdispersion index ($s^2/\bar{x}$) in different size-classes of whitefish and in fish of $\geqq$ 175 mm is length studied seasonally shows that trematodes in the whitefish of Lake Kitka are overdispersed such that overdispersion increases with increasing length of the fish (Tables 2 and 3). When examinig the nature of the overdispersion in more detail, frequency distributions were counted and a negative binomial distribution fitted. This gave a satisfactory fit in the two largest size-classes for the combined material and also during a limited period for the fish of $\geqq$ 175 mm in length. Parameter k for the negative binomial parameters is very small in all cases (between 0.1—0.3) (Tables 2 and 3, Fig. 6).

Table 2. Data for the frequency distributions of *Crepidostomum* spp. in the whitefish of Lake Yli-Kitka according to the length of fish and parameters of fitted negative binomials. That marked with • is plotted in Fig. 6

Length group (mm)	No. of fish	Prevalence %	Mean $\bar{x}$	Variance s^2	$s^2/\bar{x}$	p	k	pkq	X^2 prop.
$\leqq$ 174	242	4.1	0,14	0.82	5.9	too few classes			
175—204	119	16.0	0.82	5,85	7.1	8.2	0.1	7.5	0.07
• $\geqq$ 205	56	42.9	2.0	22.47	11.2	8.3	0.2	18.7	0.07•

Table 3. Data for the frequency ditributions of *Crepidostomum* spp. in the whitefish (size $\pm$ 175 mm) of Lake Yli-Kitka according to the season and parameters of the fitted negative binomials. Those marked • are plotted in Fig. 6

Date	No. of fish	Prevalence %	Mean $\bar{x}$	Variance s^2	$s^2/\bar{x}$	p	k	pkq	X^2 prop.
•III 80—X 82	168	24.4	1.21	11.72	9.7	10.5	0.1	13.9	0.14•
•III 80—VIII 80	48	41.7	1.81	11.86	6.6	6.0	0.3	12.8	0.29•
IX 80—I 81	55	9.1	0.27	1.20	4.4	too few classes			
II 81—VI 81	31	25.8	1.03	7.63	7.4	too few classes			

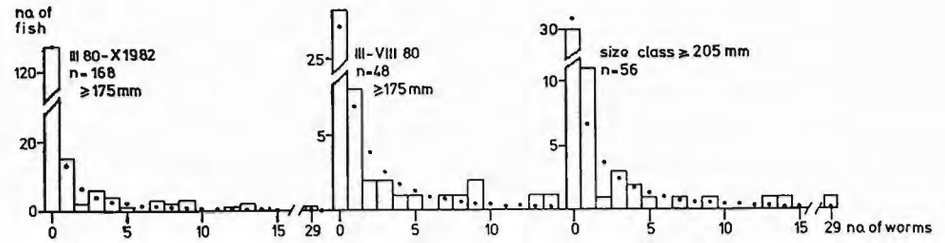

Fig. 6. Frequency distribution of *Crepidostomum* spp. in whitefish from Lake Yli-Kitka of the size group $\geqq$ 175 mm for the combined material and between March and August 1980, and for the size-class $\geqq$ 205.

DISCUSSION

The vendace of Lake Yli-Kitka seem to be of little importance as a final host of *Crepidostomum farionis*, although worms are capable of becoming gravid in this fish. The vendace of Lake Yli-Kitka feed mainly on plankton (Rintamäki, unpubl.) so the second intermediate host of *Crepidostomum*, an insect larva, is probably too large for them. In the lake the most important definitive hosts are whitefish and brown trout. Several authors in the neighbouring Soviet Karelia have found the prevalence of *C. farionis* infection in coregonids to be similar or lower than that found in the present study (see Petrushevski 1940, Barysheva and Bauer 1957, Nagibina 1957, Shulman et al. 1974, Ieshko et al. 1982, Permyakov and Rumyantsev 1982, Anikieva et al. 1983). Although the prevalence in the whitefish of Lake Yli-Kitka is only about 13 %, it is high when compared to the results of some other studies made in Canada. For example 5 % or less of the lake whitefish *Coregonus clupeaformis* (Mitchill) were infected with *C. farionis* in coastal Labrador (Hicks and Threlfall 1973), in Smallwood Reservoir, Labrador (Chinniah and Threlfall 1978) and in Cold Lake, Alberta (Leong and Holmes 1981).

As the infected brown trout of Lake Yli-Kitka are predatory fish, they presumably have acquired the worms by ingesting vendace and whitefish. Although a low infection of *Crepidostomum* is found in the vendace of Lake Yli-Kitka, it may have importance in transmitting these trematodes to brown trout. Vendace is the most common fish species in the lake (Hyytinen 1985) and it is among the most frequent items in the diet of brown trout in Lake Yli-Kitka (L. Hyytinen, unpubl.). One kilogram of vendace contains 189 specimens (mean weight 5.3 g) and extrapolation of our results indicate that they would be expected to contain 1.7 specimens of *Crepidostomum*. The phenomenon of a higher level of infection of *C. farionis* in *Salmo* species than in *Coregonus* species, as occurs in Lake Yli-Kitka, is also found elsewhere, e.g. in *Salmo* and/or *Salvelinus* species in Canada (Hicks and Threlfall 1973, Hare and Burt 1975, Chinniah and Threlfall 1978) and in Soviet Karelia (Ieshko et al. 1982).

Previously *C. farionis* has been observed in Finland by Jääskeläinen (1911), who found this species in 7 % of the lake salmon (*Salmo salar* m. *sebago* Girard) in Lake Höytiäinen in eastern Finland and two specimens from the intestine of grayling (*Thymallus thymallus* (L.)) from the River Kemijoki in northern Finland (Jääskeläinen 1913a, b). Jokikokko (unpubl.) found *C. farionis* in brown trout (*Salmo trutta* m. *fario* L.) in the streams of the River Iijoki in northern Finland. In addition Rahkonen (unpubl.) has reported *C. farionis* in 16 % and 32 % of the whitefish

and 2 % and 12 % of the vendace of two small lakes close to tributaries of the River Tornionjoki. All these rivers flow into the Bothnian Bay, where the species, however, has not been found (Valtonen et al. 1984).

The large-egged species, *Crepidostomum wikgreni*, occurring mainly in the gall-bladder but also in the intestine of *Coregonus acronius*, occurs sympatrically and even concurrently in the same fish with *C. farionis* and its origin poses a problem. According to Gibson and Valtonen (1988) the absence of evidence that *C. wikgreni* occurs elsewhere suggests strongly that it is the endemic form. Its close morphological similarity with *C. farionis* indicates that it has probably evolved from this species. Gibson and Valtonen propose the followig interesting scenario of the events which might explain the current situation: "After deglaciation *C. farionis* extended its range into the Baltic and White Sea Basins, and then from the Baltic region via River Livojoki into the Lake Kitka System. After the severage of the Baltic connection at about 8400 BP this worm evolved in isolation into the new form, *C. wikgreni*. The *C. farionis* currently in the system is a recent reintroduction brough about by the translocation fish-stocks".

The lack of worms in the smallest and youngest whitefish in the present study may be due to the paucity of the second intermediate hosts in the diet of the small whitefish or because small fish occur in areas where the second intermediate hosts are not found. Second intermediate hosts which have been incriminated include *Gammarus pulex* L. (Thomas 1958, Awachie 1968), *Ephemera danica* Müller (Brown 1927, Anikieva et al. 1983), *Siphlonurus occidentalis* Eaton, *Callibaetis* sp., *Tricorythoides* sp. and *Paraleptophlebia* sp. (Klein and Olsen 1969). None of these species has been found for certain from Lake Kitka System (Kuusela, in litt.). *C. metoecus* (Braun, 1900) has been observed concurently with *C. farionis* (Thomas 1957, 1958, Awachie and Chubb 1964, Awachie 1968, Moravec 1982, Mariaux 1986) and, according to Awachie (1968), they share the same second intermediate host, *Gammarus pulex*. Increased levels of *Crepidostomum* infection associated with increasing length of the fish as found in this study have also been found by Thomas (1957, 1958) in *Crepidostomum metoecus* and *C. farionis* from *Salmo trutta* L. and *S. salar* L. in mid-Wales, by Bwathondi (1976) in *C. metoecus* from *Salmo trutta* L. in N. E. Scotland, by Watson and Dick (1979) in *C. farionis* from whitefish (*C. clupeaformis*) in Manitoba, Canada and by Moravec (1982) in *C. metoecus* from *Salmo trutta* m. *fario* L. in Southern Bohemia, Czechoslovakia. The prevalence and the mean intensity of infection were significantly higher in salmonids than in whitefish of Lake Yli-Kitka (see Thomas 1958, Bwathondi 1976, Moravec 1982). Nevertheless, Hare and Burt (1975) did not find consistent trends in the prevalence and intensity of *C. farionis* infection when plotted against the age of *Salmo salar* L. in New Brunswick, Canada when analysed seasonally. In this study, however, a very clear increase was also observed in the prevalence of infection in three different seasons.

Unlike the small whitefish in Lake Yli-Kitka, *Crepidostomum* infections have been reported in *Salmo* spp. in the smallest and youngest (age $0^+ - 1$) fish (Thomas 1957, 1958, Hare and Burt 1975, Bwathondi 1976, Moravec 1982). This is presumably due to differences in diet of the fry of *Salmo* spp. and *Coregonus* spp.

Information about the seasonal occurrence of *C. farionis* and *C. metoecus* was available only from *Salmo* spp. According to studies of Thomas (1957, 1958), Awachie and Chubb (1964), Awachie (1968), Hare and Burt (1975), Bwathondi (1976) and Moravec (1982), the seasonal rhythm is very clear: the prevalence of infection is low in summer months, increases in autumn and is at its highest level in the winter and spring. In this study a similar trend was clearly observed both in the prevalence and mean intensity of infection in 1982, and also in 1980—1981, except for the fact

that the gap between generations occurred later, in the autumn. Similar variation in the level of infection of a related species, *Bunodera luciopercae*, was found in northern latitudes by Rahkonen et al. (1984).

With regard to the seasonal variation and developmental cycle of *Crepidostomum* in the whitefish of Lake Yli-Kitka, it is suggested that the main recruitment time is the autumn and early winter (August-December), but invasion also occurs in spring and even in summer. This indicates that the infected second intermediate hosts are available throughout the year as it is stated also by Frimeth (1987) in *C. farionis* from brook charr (*Salvelinus fontinalis*) in New Brunswick, Canada. Eggs mature during late spring and summer. Moravec (1982) assumed that the metacercariae of *C. metoecus* obtained by trout during the winter, spring and summer seasons gradually start to mature in the summer, but mainly in the autumn, and survive in the host until the spring months of the following year: the trematodes obtained in the autumn probably mature in early spring. This cannot be the case in the present study where there is a clear gap in the prevalence of infection, such that the worms ingested in the spring and early summer mature before September. The presence of immature worms throughout the winter may also indicate that the long, cold winter retards the development of the worms. The reason for the break in the invasion in January and February in 1980 and 1982 may be due to winter starvation, which is known to occur in *Coregonus acronius* in Lake Yli-Kitka (Rintamäki, unpubl.) and also in *Coregonus widegreni* Malmgren, 1863 (syn. *C. nasus*) in the Bothnian Bay (Valtonen and Valtonen 1980). A clear annual maturation cycle as in this study was also observed by Awachie and Chubb (1964) and by Awachie (1968) in *C. farionis* and *C. metoecus* from brown trout (*Salmo trutta* L.) in north Wales, and also by Hare and Burt (1975) in *C. farionis* from Atlantic salmon, although their study lasted only from May to November.

Published results on the distribution of *C. farionis* in the intestine of fish vary. According to Brown (1927), Klein and Olsen (1969), Hare and Burt (1975) and Chinniah and Threlfall (1978), immature *C. farionis* occur in the anterior part of the intestine, the pyloric caeca and rarely in the gall-bladder. Thomas (1957, 1958), Awachie (1968) and Moravec (1982) indicate that *C. farionis* occurred in the posterior part of the intestine, whereas *C. metoecus* were present mostly in the pyloric caeca and anterior part of the intestine. Mariaux (1986) recorded 28.7 % of *C. farionis* from gall-bladder of *Salmo trutta* m. *fario*, none from the pyloric caeca, 6.6 % from intestine and 64.7 % from rectum over the course of a year. *C. metoecus* was found concurrently as follows: 5.6 % from gall-bladder, 53.2 % from pyloric caeca, 34.7 % from the intestine and 6.5 % from rectum. In the whitefish of Lake Yli-Kitka mature specimens of both species of *Crepidostomum* occurred in the intestine and gall-bladder, although ovigerous *C. farionis* only once in the gall-bladder. According to our results a few very small worms were seen in the intestine only in the autumn, but they occurred frequently in gall-bladder especially during the autumn, early winter and in spring. This would indicate that immature worms migrate first to the gall-bladder, some of them maturing there, but later during spring and summer they migrate to the intestine. This would explain the fact that adult parasites were seen in the intestine only in spring and summer. Mariaux's (1986) results supports also the idea of migration. Mariaux's figures reveal that 9.1 % of *C. farionis* were found from the gall-bladder in January-April, 8.8 % in May-August and 46.8 % in September-December. In the case of *C. metoecus* the figures were 0 %, 3.4 %, 31 %, respectively. One would expect the high autumnal figures to reflect the influx of immature specimens.

Both the variance to mean ratio and low values of parameter k of the fitted ne gative binomial distribution reveal that *Crepidostomum* specimens are overdisper sed or

aggregated in the whitefish of Lake Yli-Kitka. The overdispersion of parasites is a very common phenomenon in nature (e.g. Kennedy 1968, Pennycuick 1971, Anderson 1974, Henrickson 1977, Valtonen and Niinimaa 1983), and it may also be obtained under controlled experimental conditions (Anderson et al. 1978). In their final and paratenic hosts this has been explained, for example, by the aggregation of larval stages in the intermediate hosts. This has been found in intermediate hosts such as naturally infected molluscs (Evans et al. 1981).

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ЭКОЛОГИЯ ВИДОВ РОДА *CREPIDOSTOMUM* (ALLOCREADIIDAE: DIGENEA) ЛОСОСЕЙ ИЗ ОЗЕРА ИЛИ-КИТКА В СЕВЕРОВОСТОЧНОЙ ФИНЛЯНДИИ

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Резюме. Виды рода *Crepidostomum* изучали в 417 сигах (*Coregonus acronicus* Rapp, 1854), 220 европейских ряпушках (*Coregonus albula* L.) и 38 кумжах (*Salmo trutta N. lacustris* (L.)) из озера Или-Китка в северовосточной Финляндии в 1980—1983 годах. 12,7 % сигов было инфицировано паразитами рода *Crepidostomum* со средней интенсивностью 4,6 червья на одну инфицированную рыбу. У сигов находили виды *C. farionis* (Müller, 1784) и *Crepidostomum wikgreni* (Gibson et Valtonen, 1988), который отличается от вида *C. farionis* количеством и размерами яйц. Оба вида встречались в желчном пузыре и кишечнике, но невозможно было отличить незрелые стадии. 21 % кумжей содержало *C. farionis* в кишечнике — в среднем 1,5 червья на одну инфицированную рыбу. Два экземпляра *C. farionis* обнаружили и в кишечнике одной европейской ряпушки. В сигах с длиной меньше 150 мм не встречались экземпляры рода *Crepidostomum*, но в рыбах больше 150 мм встречаемость и средняя интенсивность инфекции росла с увеличением размеров рыб. Встречаемость паразитов рода *Crepidostomum* в трёх изучаемых группах отличающихся по размерам увеличивалась в течении трёх сезонов. Сезонная встречаемость видов рода *Crepidostomum* в сигах больше 150 мм изменялась, самый низкий уровень (что касается встречаемости и интенсивности инфекции) наблюдали с сентября до декабря в 1980 году и с апреля до августа в 1982 году. Повторые инфекции находили в течение всего года, хотя больше всего осенью и в начале зимы. Яйца созревали с поздней весны до начала осени. Самых малых червей находили в основном в желчном пузыре, большинство экземпляров содержащих яйца располагалось в кишечнике. Оба параметра — дисперсия среднего и низкое значение коэффициента k — подходящего отрицательного биномиального распределения показывают, что экземпляры рода *Crepidostomum* распределены по группам сигов из озера Или-Китка.

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