

Occurrence of cestode larvae in brown trout after stocking in a large regulated lake in northern Finland

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ABSTRACT: The aim of this study was to obtain relevant information on larval cestode infection of brown trout *Salmo trutta* m. *lacustris*, for fish stock management purposes in the large, regulated Lake Inari in northern Finland. Compensatory stockings of brown trout have been carried out annually since the mid-1970s. A total of 209 brown trout, which were stocked at the age of 3 yr, were studied for larval cestodes in 1994 and 1995. *Diphylobothrium dendriticum* was clearly dominant among the 4 cestode larval species found. The other species were *D. ditremum*, *Triaenophorus crassus* and *T. nodulosus*. After 1 summer in the lake the prevalence of *D. dendriticum* infection was 75% (abundance 5.3) and 46% (abundance 0.9) in 1994 and 1995, respectively. After 3 or more years in the lake ($\geq 6+$) every brown trout was infected with a mean number of about 130 larvae for both years. All organs in the body cavity were found to be infected. In addition, capsules containing *D. dendriticum* were found in muscles after the second summer in the lake and the prevalence of muscle infection was 73% (abundance 3.2) and 95% (abundance 7.1) in the oldest age group ($\geq 6+$) in 1994 and 1995, respectively. This has decreased the commercial value of the brown trout. A slight positive correlation between the number of *D. dendriticum* and the condition index (Fulton) of fish was found in each age group, although histological studies of heavily infected fish revealed severe chronic granulomatous peritonitis. Indications of elimination of individuals most heavily parasitized with *D. dendriticum* were not obtained for the present material. *D. dendriticum* was not found in the potential prey fishes of the brown trout studied in Lake Inari: vendace *Coregonus albula*, whitefish *Coregonus* sp. and nine-spined stickleback *Pungitius pungitius*.

KEY WORDS: *Salmo trutta* m. *lacustris* · Brown trout · *Diphylobothrium dendriticum* · *Diphylobothrium ditremum* · *Triaenophorus crassus* · *Triaenophorus nodulosus* · Regulated lake · Stocking

INTRODUCTION

Lake Inari is a large, oligotrophic lake in northern Finland. Regulation of the water level began in the 1940s and has been shown to strongly affect the bottom fauna in the littoral zone of the lake (Toivonen 1966, Hiisivuori & Honkasalo 1977). This in turn has reduced the available food for fish, and annual catches of fish declined dramatically in the 1950s and onwards (Toivonen 1966). Since the mid-1970s, the damage to

fish stocks and fisheries obviously caused by regulation has been mitigated with annual stockings of local brown trout *Salmo trutta* m. *lacustris* (L.), for example (Mutenia 1995). Brown trout catches were high in the 1980s because of a strong vendace *Coregonus albula* L. stock which provided a good food supply for the brown trout (Mutenia 1995). Since 1991 the vendace stock, as well as the local whitefish stock, has been weak (because of the natural stock fluctuation) and for this reason the catches of brown trout have declined dramatically (Mutenia 1995). In addition, the brown trout have been infected with increasing amounts of larval cestode capsules in their body cavity and mus-

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cles, creating adverse effects on the commercial value of the fish (A. Mutenia & E. Salonen pers. comm.). Previous heavy *Diphyllbothrium dendriticum* (Nitzsch, 1824) infections were reported from Lake Inari in the 1960s (Bylund 1966), when the stocks of the predatory fish species were also very low (Mutenia 1995). However, no parasitological study has been undertaken since.

It has been suggested that the regulation of lakes tends to favour cestode populations in fish (e.g. Petersson 1971), since the destruction of littoral bottom fauna forces many fish species to feed more on plankton, including copepods, which are the first intermediate hosts for cestodes. On the other hand, Wisniewski (1958) and Esch (1971) have suggested that larval parasites which mature in birds or mammals, like *Diphyllbothrium* species, are more common in eutrophic bodies of water than in oligotrophic ones. The reports on mass occurrences of *D. dendriticum* and *D. ditremum* (Creplin, 1825) (Vik 1957, Halvorsen 1970, Bylund 1972, Henricson 1977, 1978, Curtis 1983, Bérubé & Curtis 1986, Gustafsson 1996) in salmonids suggest, however, that there might be other factors of influence in the oligotrophic northern lakes which favour *Diphyllbothrium* species.

The aim of this study was to obtain relevant information on the larval cestode infection of brown trout for fish stock management purposes. Firstly, we wanted to examine the composition and infection level of the larval cestode species, allogenic *Diphyllbothrium dendriticum* and *D. ditremum* (maturing in birds and mammals) and autogenic *Triaenophorus crassus* Forel, 1868 and *T. nodulosus* (Pallas, 1760) (maturing in fish) in brown trout in relation to the number of years after stocking in Lake Inari. According to the previous publications on the mass occurrence of *Diphyllbothrium* spp. in brown trout and Arctic char *Salvelinus alpinus* (L.) in northern lakes (see ref. above), our hypothesis was that *Diphyllbothrium* spp. would be the dominant species in Lake Inari.

Another essential question was the source of the infection in brown trout. There was only a limited amount of data available on the brown trout diet after stocking in Lake Inari; thus we considered it important to study the stomach contents of the fish as well as larval cestodes in the potential prey fishes. Planktonic copepods are the first intermediate hosts for *Diphyllbothrium* and *Triaenophorus* species, but *D. dendriticum* and to some extent also *D. ditremum* are able to re-

establish themselves from prey to predatory fishes (Halvorsen & Wissler 1973).

Pathological effects caused by *Diphyllbothrium dendriticum* leading to the mortality of fish have been demonstrated to take place at fish farms (Hoffman & Dunbar 1961, Berland 1987, Sharp 1991, Rahkonen et al. 1996) and even in lakes (Duguid & Sheppard 1944, Hickey & Harris 1947, Fraser 1960, Bylund 1972). Consequently, we surmised that a heavy infection of larval cestodes might cause negative effects to individual fish as well as the population level, thus impairing the stocking results. Our third aim was to study the pathological changes of the infected fish, and any direct or indirect (see e.g. Anderson & Gordon 1982) evidence of mortality.

MATERIALS AND METHODS

Study area. Lake Inari is a large (1102 km²) oligotrophic lake in Finnish Lapland flowing via the River Paatsjoki into the Arctic Ocean (Fig. 1). The regulation of the water level in Lake Inari began in the 1940s at power stations on the River Paatsjoki in Russia, and the water level was raised 0.5 m above its normal level (Mutenia & Salonen 1994). The maximum permitted fluctuation in water level is 2.4 m.

Fish samples. A total of 121 and 88 brown trout were caught in southern parts of Lake Inari by gill net and trawl from August to October in 1994 and 1995, respectively (Table 1). In the 1994 sample, 10 brood fish were also captured in a local river where they had migrated from Lake Inari to spawn. Potential prey fish of brown trout were taken by trawl and pound net in

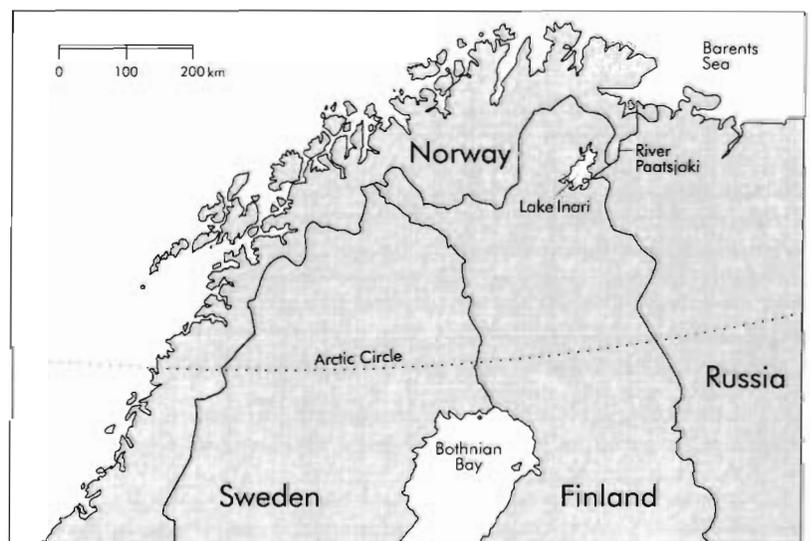


Fig. 1. Location of Lake Inari in northern Finland

1995. A total of 222 prey fish included small whitefish *Coregonus* spp., vendace, and nine-spined stickleback *Pungitius pungitius* (L.). The fish were put into ice (about 0°C) after capture. Most of the brown trout had been deep-frozen before their study in 1994, while in 1995 most of them (61/88) and all prey fish were studied fresh.

Examination of fish. The total length and weight of the brown trout was recorded and age determination was based on the scales. For several years only 3-yr-old brown trout have been used for stocking. Consequently, at the time they were caught in autumn, fish aged 3+ had spent 1 summer in Lake Inari, those 4+ had spent 1 year plus 1 summer, and so on. The fish were opened, and sex and gonad developmental stages were assessed (Nikolsky 1963). The stomach of each brown trout was studied and the food items recorded macroscopically as follows: plankton, surface animals, bottom animals, and fish by species as far as possible.

Visible parasite capsules on the stomach, on and between pyloric caeca and other visceral organs were removed, counted and studied at 7 to 10× magnification using transmitted light. The stomach wall was studied thoroughly in order to find small capsules and small unencapsulated larvae in 1995. The pericardial cavity was opened and the cavity and heart were studied. Finally the skin was removed, the flesh was cut into 0.5 cm slices and the worms and capsules were studied.

Larval cestodes were also examined from the visceral organs of potential preyfishes: 86 small whitefish, 85 nine-spined stickleback and 51 vendace.

Live *Diphylobothrium* larvae were fixed in 70% ethanol; worms from frozen fish were transferred to tap water for an hour and after species identification were preserved in 70% ethanol. *Triaenophorus* species were identified from the hooks.

Pathology. A normal pathoanatomical necropsy procedure was performed on 6 heavily infected brown trout (length 35 to 49 cm, weight 401 to 1063 g) caught in September 1995. Of the organs with macroscopic lesions, samples for histology were taken into phosphate-buffered 10% formalin. Normal paraffin embedding was done after dehydration through a graded series of ethanol. Slices of 3 µm thickness were stained with haematoxylin and eosin (Humason 1979).

Statistics. Computations were carried out with SYSTAT statistical software (SYSTAT 1992). For the fully factorial ANOVA model the normality

of the residuals was tested with Lillefors' test and the homogeneity of variances with Cochran's test (Day & Quinn 1989). However, in most cases valid assumptions for parametric tests were not obtained. In these cases non-parametric tests, Mann-Whitney *U* or Kruskal-Wallis tests, were used. Differences in frequencies were tested with the likelihood ratio chi-square (G^2) test and correlations with Spearman's rank correlation test.

RESULTS

Occurrence of larval cestodes in brown trout

Among the larval cestode species in brown trout, *Diphylobothrium dendriticum* dominated, having high prevalences (83 to 90%) and abundances (about 50 larvae per fish studied) in both years (Table 1). In 1995, *D. ditremum* appeared in and on the stomach wall of every other brown trout but the abundance, 2.5, was low compared to *D. dendriticum*. In addition, a small number of very small, unidentified *Diphylobothrium* larvae were encountered in the stomach wall. The amounts of *D. ditremum* as well as *Diphylobothrium* sp. may be underestimated for 1994 since the method used then did not reveal the larvae inside the stomach wall. The allogenic species *D. dendriticum* and *D. ditremum* were far the more abundant than autogenic species, *Triaenophorus nodulosus* and *T. crassus*. *T. nodulosus* occurred in low numbers on the body cavity organs (7 and 11.5% in 1994 and 1995, respectively) and *T. crassus* in the muscles (5 and 1.1%) of the brown trout (Table 1).

In the infracommunities of brown trout (see Esch et al. 1990) the number of larval cestode species per fish increased with the age of the brown trout in 1995 (Fig. 2).

Table 1. *Salmo trutta* m. *lacustris*. Occurrence of larval cestode species in brown trout in Lake Inari in 1994 and 1995

Species		1994	1995
		No. of fish: Length, cm:	121 35.0
<i>Diphylobothrium dendriticum</i>	Prevalence %	90.0	83.0
	Abundance (SD)	52.9 (70.4)	50.2 (82.1)
<i>D. ditremum</i>	Prevalence %	21.0 ^a	52.9
	Abundance (SD)	0.5 (1.3) ^a	2.5 (7.2)
<i>Diphylobothrium</i> sp.	Prevalence %	— ^a	10.2
	Abundance (SD)	— ^a	0.2 (0.5)
<i>T. nodulosus</i>	Prevalence %	7.4	11.5
	Abundance (SD)	0.2 (1.1)	0.2 (0.5)
<i>T. crassus</i>	Prevalence %	5.0	1.1
	Abundance (SD)	0.1(0.4)	0.02 (0.2)

^aLarval cestodes inside the stomach wall were not studied

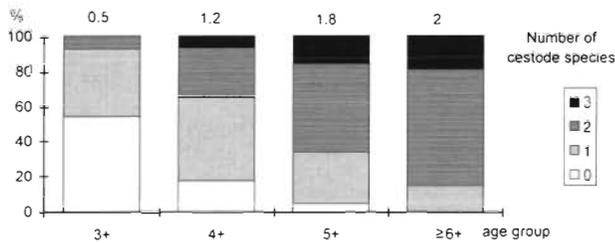


Fig. 2. *Salmo trutta m. lucustris*. Number of larval cestode species in brown trout in different age groups in Lake Inari in 1995. The mean number of species is indicated above the column

Occurrence of *Diphyllbothrium dendriticum* in relation to fish age

The relationship between fish age and the occurrence of *Diphyllbothrium dendriticum* larvae was studied in 4 age groups of brown trout. Prevalence increased in relation to age in both 1994 and 1995 ($G^2 = 12.830$, $df = 3$, $p = 0.005$ and 19.080 , $df = 3$, $p < 0.001$, respectively) (Fig. 3). When compared by age group, the prevalences of infection were the same in both years (G^2 -test, $p > 0.05$ in all cases).

The mean abundance of infection also increased significantly with fish age in 1994 and 1995 (Kruskal-Wallis test statistic 56.212 and 58.612, respectively, $df = 3$, $p < 0.001$) and the distributions were overdispersed (variance > mean) (Table 2). The variance-to-mean ratio dropped in the oldest age group in 1994 while it increased in the same age group in 1995. When adjusted to number of comparisons, abundances were statistically significantly lower in the 3+ age group in 1995 compared to 1994 (Mann-Whitney U test statistic 122.500, $df = 1$, $p = 0.012$), but there were no significant differences in older age groups.

At the end of the first summer in the lake (age 3+) small *Diphyllbothrium dendriticum* larvae were found mostly unencapsulated within the tissues of the outer

surface of the stomach (Fig. 3). After the second lake summer (4+) most of the larvae were in capsules on the stomach and other body cavity organs and the first worms were found in the muscles (i.e. clearly under the body wall). The occurrence of larvae in muscles increased with fish age, the prevalence being 73% (abundance 3.2, SD 3.4) in 1994 and 95% (abundance 7.1, SD 10.2) in 1995 after at least 4 summers in the lake (age $\geq 6+$). *D. dendriticum* capsules were encountered in the lateral muscles only within the area downwards from the lateral line and in front of the ventral fins.

In the atrium of the heart 1 or 2 larvae were found mostly unencapsulated in about 13% of the 5+ trout in both years and in 5% of the $\geq 6+$ trout in 1995. In addition, some encapsulated larvae were found in the pericardium in 3 to 20% of the 4+ and older trout.

Fulton's condition index [total weight(g) \times 100/total length(cm)³] varied in age groups between 0.92 and 1.03. It seemed to increase with age except for age 4+, when it dropped both years. The increase was significant in 1995 (ANOVA, $F_{(3, 82)} = 5.37$, $p = 0.002$). The number of *Diphyllbothrium dendriticum* larvae and the condition index correlated positively but not statistically significantly in each age group in both years (Spearman's rank correlation test, $p > 0.05$). The brood fish were omitted from the condition examination because of heavy, mature gonads. All other fish had small, immature gonads: stages 0 to 3, using a scale of 1 to 6 according to Nikolsky (1963).

The scale analyses revealed that 8 fish aged 6+ and older originated from wild spawners in 1994 material. Seven of them were captured as brood fish from a river draining into Lake Inari. These wild fish were excluded from the former examination and a separate comparison was made between them and those aged 6 yr and older which had been stocked into the lake as 3-yr-olds ($n = 15$). The number of *Diphyllbothrium dendriticum* larvae was significantly lower in wild fish than in stocked fish (Mann-Whitney U test statistic 107 000, $df = 1$, $p = 0.002$).

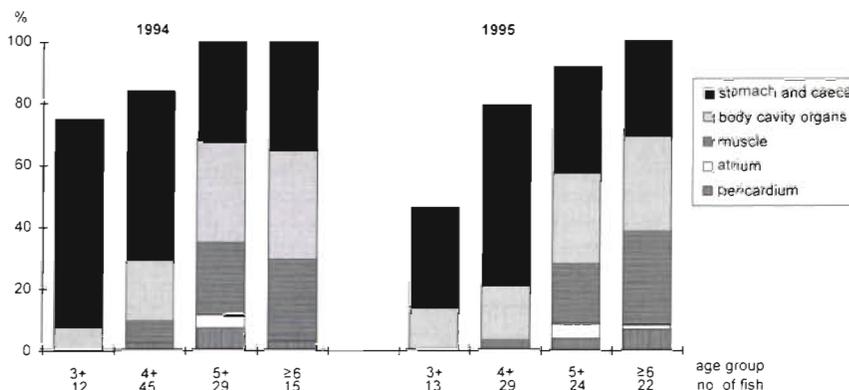


Fig. 3. *Salmo trutta m. lucustris*. Prevalence of infection and occurrence of *Diphyllbothrium dendriticum* in different organs (in proportion to the height of the column) of brown trout by age group in Lake Inari in 1994 and 1995

Table 2. *Salmo trutta m. lacustris*. Occurrence of *Diphyllbothrium dendriticum* in brown trout in different age groups in Lake Inari in 1994 and 1995

Age	1994							1995						
	No. of fish	Mean length	Abundance:		Min	Max	Var/mean	No. of fish	Mean length	Abundance:		Min	Max	Var/mean
			Abun.	SD						Abun.	SD			
3+	12	26.5	5.3	5.0	0	16	4.7	13	24.5	0.9	1.4	0	5	2.3
4+	45	31.9	17.2	21.7	0	97	27.4	29	28.9	7.4	14.5	0	65	28.4
5+	29	37.3	86.9	83.1	4	326	79.6	24	36.1	53.2	57.9	0	258	63.0
≥6+	15	53.4	128.7	72.8	33	258	41.1	22	45.1	132.3	113.6	27	425	97.5

Pathology

All 6 brown trout subjected to the pathoanatomical examination were heavily infected and had severe chronic granulomatous peritonitis. The strongest granulomatous reactions were found in fish which had the greatest number of *Diphyllbothrium* plerocercoids, especially in the region of the pancreas and pyloric caeca. Fibrinous adhesions between the visceral organs and the parietal peritoneum were present in 4 fish.

Food composition in brown trout in 1995

Animals collected from the surface waters, primarily ants, were the most common food items in the smallest size class. The proportion of fish in stomachs increased rapidly as the fish grew (Fig. 4). Nine-spined stickle-

back was clearly the most abundant prey fish species and its proportion compared to *Coregonus* species increased to almost 100% among fish aged 6+ and older.

Occurrence of larval cestodes in prey fish

Diphyllbothrium dendriticum was not found in any of the prey fish studied. Very small, unidentified *Diphyllbothrium* larvae occurred in and on the stomach wall of whitefish aged 0+ (length <7.5 cm) (Table 3). Some *D. ditremum* larvae as well as small unidentified *Diphyllbothrium* specimens were found in 20% of the whitefish older than 1 yr. A few *D. ditremum* larvae occurred frequently in the liver of the nine-spined stickleback, and *Schistocephalus* sp. and *T. nodulosus* were also observed (Table 3). Larval cestodes did not occur in the 51 vendace studied.

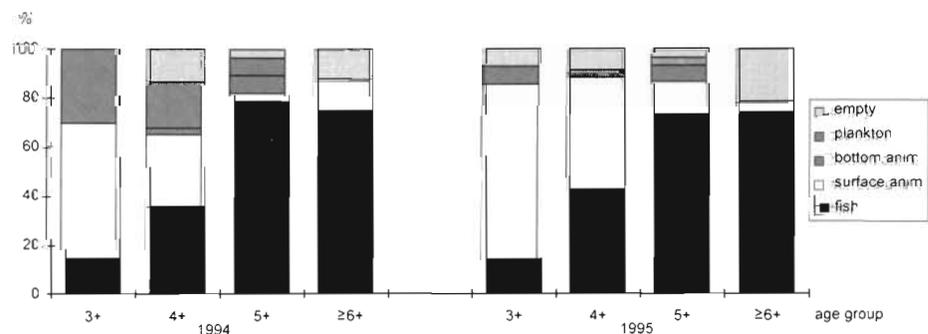


Fig. 4. *Salmo trutta m. lacustris*. Food composition of brown trout by age group proportioned to 100% in Lake Inari in 1994 and 1995

Table 3. *Salmo trutta m. lacustris*. Larval cestode species in the potential prey fish of brown trout in Lake Inari in 1995

	n	Mean length (cm)	<i>Diphyllbothrium dendriticum</i>			<i>Diphyllbothrium</i> sp.			<i>Schistocephalus</i> sp.			<i>Triaenophorus nodulosus</i>		
			Prev. (%)	Abun.	SD	Prev. (%)	Abun.	SD	Prev. (%)	Abun.	SD	Prev. (%)	Abun.	SD
Whitefish 0+	44	6.3	0	0	0	6.8	0.07	0.3	0	0	0	0	0	0
Whitefish 1+–2+	42	10.2	21.4	0.3	0.7	14.3	0.3	0.7	0	0	0	0	0	0
Nine-spined stickleback	85	4.7	54.1	1.9	2.9	0	0	0	17.7	0.2	0.6	8.2	0.1	0.3

DISCUSSION

Parasite communities in salmonids have proved to be mostly dominated by autogenic parasite species and individuals (Esch et al. 1988, Hartvigsen & Halvorsen 1993). However, Hartvigsen & Halvorsen (1993) expected allogenic *Diphyllbothrium* spp. to be the core species in Norway, based on former studies by Halvorsen (1970), but *D. dendriticum* and *D. ditremum* occurred in small amounts in only 1 out of the 4 lakes studied. Although parasitological study in the present case was restricted only to the larval cestodes, allogenic *Diphyllbothrium* species occurred in such great numbers that it could be assumed they were the most abundant helminth species in the brown trout studied, at least in the 2 oldest age groups. Curtis (1983) compared the level of *Diphyllbothrium* infection in Arctic char in 4 lakes in Canada and concluded that the differences in prevalence and intensity of infection between the lakes are related to the food web structures, which are influenced for instance by the number and composition of fish species in the lake. In the lakes inhabited only by Arctic char and sticklebacks, a significant proportion of the char population may become piscivorous and heavily parasitised with *Diphyllbothrium* by transmission from prey fish (Curtis 1983). However, no detailed study of the factors which lead to heavy infection of brown trout and Arctic char (Vik 1957, Halvorsen 1970, Bylund 1972, Henricson 1977, 1978, Curtis 1983, Bérubé & Curtis 1986, Gustafsson 1996) in some northern lakes with either *D. dendriticum* or *D. ditremum* has been undertaken.

Diphyllbothrium dendriticum was clearly more abundant than *D. ditremum* in the present study. This was also the case in the 1960s, when *D. dendriticum* had a 90% prevalence in brown trout with an abundance of 100 plerocercoids (Bylund 1966). *D. dendriticum* and *D. ditremum* usually share the same copepod and fish species as first and second intermediate hosts (Hickey & Harris 1947, Halvorsen 1966, 1970, Bylund 1973, Henricson 1977, 1978, Curtis 1983, Andersen et al. 1987, Andersen & Gibson 1989, Andersen & Valtonen 1992). Many copepod species which have been proved to serve as intermediate hosts for *D. dendriticum* and *D. ditremum* occur in Lake Inari: *Cyclops abyssorum* Sars, *C. lacustris* Sars, *C. scutifer* Sars, *C. strenuus* Fischer and *Eudiaptomus gracilis* Sars (Hakkari & Selin 1980). A remarkable difference in the life-cycle strategies of *D. dendriticum* and *D. ditremum* is, however, that the ability of plerocercoids to pass from prey fish to predatory fish is well developed in *D. dendriticum* while poor in *D. ditremum* (Vik 1957, Halvorsen 1970, Halvorsen & Wissler 1973). As was seen in the present study in stomach samples of the brown trout, planktonic food decreased with

the age of the fish and was replaced by small fishes. Although *D. dendriticum* was not found in the present data in vendace, small (stunted) whitefish or nine-spined stickleback, transmission from prey fishes with low infection levels might cause accumulation of worms in brown trout. In addition, infected copepods in the stomach of any prey fish could also transport proceroids to more suitable intermediate hosts such as brown trout.

The prevalence and abundance of *Diphyllbothrium dendriticum* infection increased in relation to the age of the fish so that the mean number of capsules in brown trout of 6 yr and older was as high as 130. However, according to the present results the infection level was lower for fish aged 3+ in 1995 than in 1994, which might indicate a decrease in the exposure to *D. dendriticum* larvae. When 42 brown trout aged 4+ were studied for *D. dendriticum*, both the prevalence (50%) and abundance of infection (2.5) remained at a low level in 1996 (Mutenia et al. 1997) compared to 1994 and 1995. The dynamics of *D. dendriticum* infection will be monitored annually as part of other studies in Lake Inari for the next several years to verify the alterations in the infection level relative to other changes such as variations in vendace and whitefish populations.

In the present data, a great proportion of the brown trout of a size of commercial value had *Diphyllbothrium dendriticum* in their muscles, which has an impact on the human consumption of the brown trout. According to the regulations of the Ministry of Agriculture and Forestry in Finland (5/EEO/94), fish purchased for human consumption must not contain visible parasites in their body cavity and muscle after gutting. *D. dendriticum* may be of particular importance as a human parasite in the Arctic and Subarctic regions (Curtis & Bylund 1991). Its infectivity to humans has been demonstrated by Vik (1957), Bylund (1969), Halvorsen (1970) and Rausch & Hilliard (1970). The growing popularity of lightly salted or inadequately cooked ethnic fish dishes, especially salmon, along with improved transportation systems, caused an increase in human diphyllbothriasis in Canada and the US in the 1980s (Ching 1984, Ruttenberg et al. 1984). However, thorough epidemiological studies on *D. dendriticum* in humans are still needed in light of the present results.

The mortality of stocked brown trout and rainbow trout due to *Diphyllbothrium* infection has been demonstrated in the British Isles (Duguid & Sheppard 1944, Hickey & Harris 1947, Fraser 1960) and in vendace in 1 eastern Finnish lake (Bylund 1972), but has not been found in Lake Inari. Even relatively small numbers of *D. dendriticum* have proved to be fatal in experiments as well as at fish farms (Kuhlov 1953, Hoffman & Dunbar 1961, Bylund 1969, 1972, Rah-

konen et al. 1996). *D. dendriticum* caused mortality, as high as 18%, at a fish farm about 100 km southwest of Lake Inari in the 1990s after migrating into the heart of sea trout *Salmo trutta* m. *trutta* (L.) and brown trout (Rahkonen et al. 1996). In the present data some brown trout aged 4+ and older also harboured encapsulated *D. dendriticum* larvae in the pericardium and $\leq 13\%$ 5+ and older had unencapsulated larvae even in the atrium. Thus, the role of larvae migrating into vital organs as a cause of mortality in the current brown trout population can neither be proved nor excluded, but needs to be studied experimentally.

Indirect evidence of the mortality of heavily parasitized individuals in the wild can be seen as a decrease in the degree of overdispersion within the older age classes of the hosts, concomitant with a decline in mean abundance (Anderson & Gordon 1982). The latter authors used Henricson's (1977, 1978) data, and data from others, to suggest that the observed decrease in the mean abundance and the variance-to-mean ratios of *Diphyllbothrium dendriticum* and *D. ditremum* in the oldest age groups in Arctic char was the result of host death. In the present data the variance-to-mean ratio decreased in the oldest age group in 1994 material, but the abundance of infection increased, so there was no evidence that the most heavily parasitized individuals were being eliminated from the brown trout population.

A somewhat surprising result was that the number of *Diphyllbothrium dendriticum* larvae and Fulton's condition index of the fish had a slight positive correlation; it seems that the more a fish eats, the more larvae it accumulates. On the other hand, the larvae and their capsules also increase the weight of the fish and because of this it would have been useful to measure the gutted weight. Heavily infected brown trout suffered from a severe inflammatory reaction in the body cavity but its real impact on condition or mortality could not be proved.

The results obtained in this study support the suggestion by local fish biologists that the number of stocked brown trout should be considerably reduced when the food supply, i.e. vendace and whitefish stocks, is poor in Lake Inari. An interesting observation in the present data is, however, that the infection level in wild brown trout was clearly lower than in stocked fish of the same age. One reason for this might be that wild fish avoid *Diphyllbothrium dendriticum* infection while spending 4 to 5 yr as parrs in local rivers (see e.g. Rahkonen et al. 1996) before they enter the lake. Another explanation could be differences in the diets of wild and farmed fish. In the light of this result, increasing of brown trout stockings in rivers instead the lake might hinder, at least to some extent, *D. dendriticum* infection, but this needs to be studied.

In conclusion, the allogenic larval cestodes *Diphyllbothrium dendriticum* and *D. ditremum* were clearly more abundant than the autogenic *Triaenophorus nodulosus* and *T. crassus* in the stocked brown trout in Lake Inari. *D. dendriticum* was the dominant species and its prevalence and abundance increased with the age of the fish, concomitant with the increasing proportion of prey fish in the stomach contents. However, *D. dendriticum* was not found in the prey fish species studied: whitefish, vendace and nine-spined stickleback. Two years after stocking and onwards, *D. dendriticum* often occurred in the muscles of brown trout, decreasing the commercial value of the fish. Direct or indirect evidence of *D. dendriticum* induced mortality was not found. There was a slight positive correlation between the number of plerocercoids and Fulton's condition index of the fish, although the heavily infected fish suffered from severe granulomatous peritonitis.

As stated by Esch & Fernández (1993), empirical evidence to support parasite-induced host mortality in natural populations is not extensive, although some examples do exist. It is very difficult to differentiate the effects of many factors contributing to fish mortality in natural environments. One way of obtaining more detailed data about the effect of helminth parasites, *D. dendriticum* for instance, on the welfare of the host fish is to approach this subject using laboratory experiments.

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