

Infection levels of plerocercoids of the tapeworm *Triaenophorus crassus* and feeding strategy in two fish species from the ultra-oligotrophic Lake Achensee, Austria

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Abstract

Thus far, high burdens of *Triaenophorus crassus* plerocercoids have been reported only in old age groups of coregonid and salmonid fishes. Here we show heavy infection with *T. crassus* in young whitefish *Coregonus lavaretus* in the ultra-oligotrophic and regulated Achensee in Tyrol, Austria. Prevalence of *T. crassus* on *C. lavaretus* was 100% in all age groups and abundance significantly increased with fish age. The mean annual accumulation of *T. crassus* was 5.2 parasites in 0- to 7-year-old *C. lavaretus*, and 2-year-old specimens already harboured a mean of 19.4 plerocercoids. In Arctic charr *Salvelinus umbla*, however, the prevalence of *T. crassus* was less than 16% and the majority of infected fish contained only one or two plerocercoids. *Triaenophorus nodulosus* was present neither in *C. lavaretus* nor in *S. umbla*. We assume that the heavy *T. crassus* infection in *C. lavaretus* is largely related to their zooplankton-dominated diet and to the characteristics of Achensee, while habitat choice and feeding strategy of the *S. umbla* population are seen to be the main reasons for their low burdens of *T. crassus*.

Introduction

Fishermen, managers and fishery scientists face a serious set of problems once the pseudophyllidean cestode *Triaenophorus crassus* Forel becomes established in a given water body. Although *T. crassus* does not present a hazard to human health, the parasite causes extensive financial damage to inland fisheries; plerocercoids of this parasite invade the muscle tissue of coregonid and salmonid fishes, which represent the second intermediate hosts (Kuperman, 1981; Schäperclaus, 1990). Thus, the normally highly valuable flesh cannot be marketed due to its unappetizing appearance. The commercial whitefish fishery in our study site, Lake Achensee, had to be closed due to this parasite. Apart from the considerable economic loss in the largest lake of Tyrol, Austria, *T. crassus* might also negatively affect

survival and growth of these intermediate fish hosts (Rosen & Dick, 1984; Pulkkinen & Valtonen, 1999; Sichrowsky *et al.*, 2013).

The life cycle of *T. crassus* involves two intermediate hosts and one definitive host. Copepods, the first intermediate hosts, are infected with procerocoids of *T. crassus* for only one brief period each year (Pulkkinen *et al.*, 1999; Lahnsteiner *et al.*, 2009; Sichrowsky *et al.*, 2013). Coregonid and salmonid fishes are the predominant second intermediate hosts of *T. crassus* plerocercoids and the parasite is transmitted to them via infected copepods (Pettersson, 1971; Kuperman, 1981; Schäperclaus, 1990). The plerocercoids are able to live for several years in their second intermediate hosts (Miller, 1945b; Rosen & Dick, 1984) and the life cycle of *T. crassus* is completed when pike *Esox lucius* L. feed on infected fish. In the intestine of *E. lucius* the plerocercoids then develop into mature tapeworms, which release their eggs during spring (Miller, 1945a; Kuperman, 1981; Lahnsteiner *et al.*, 2009).

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Triaenophorus nodulosus, a congener of *T. crassus*, has a wider range of second intermediate hosts and often occurs in the same water body as *T. crassus* (Miller, 1945a; Kuperman, 1981; Lahnsteiner *et al.*, 2009; Sichrowsky *et al.*, 2013). The life cycle of *T. nodulosus* is similar to that of *T. crassus*, with the exception that the plerocercoids of *T. nodulosus* encyst in the liver of the second intermediate host (Miller, 1945a; Kuperman, 1981; Schäperclaus, 1990) and thus the fish fillets can still be marketed. Lahnsteiner *et al.* (2009) reported that *Coregonus* sp. is vulnerable to both *T. crassus* and *T. nodulosus*.

Triaenophorus crassus infection has been studied in various types of lakes and in different countries (Miller, 1945a; Petersson, 1971; Kuperman, 1981; Amundsen & Kristoffersen, 1990; Pulkkinen & Valtonen, 1999; Achleitner *et al.*, 2009). Comparing these studies, it is noticeable that the pattern of infection in second intermediate hosts can vary between lakes. It is well known that biotic, physico-chemical and morphometric characteristics of a water body play a fundamental role in structuring the parasite assemblage in coregonid and salmonid fishes (Marcogliese & Cone, 1991; Karvonen & Valtonen, 2004; Goater *et al.*, 2005). Especially the trophic status of lakes (Kuperman, 1981; Molzen, 2005; Brinker & Hamers, 2007) and the strength of trophic interactions between the hosts (Petersson, 1971; Kuperman, 1981; Amundsen & Kristoffersen, 1990) are considered to influence the intensity of *Triaenophorus* spp. infections. Nevertheless, it is not possible to make reliable predictions of the pattern of *T. crassus* infection in a given lake, not least because the primary second intermediate host can differ between lakes (Pulkkinen *et al.*, 1999; Achleitner *et al.*, 2009). Predictions are further impeded by the fact that only a few studies (Petersson, 1971; Pulkkinen & Valtonen, 1999) have investigated in depth the *T. crassus* infection in different age groups of coregonid and salmonid fishes. Therefore, more detailed information on the infection dynamics and the pattern of *T. crassus* infections is a prerequisite for further parasite control measures.

The primary aim of this study was to investigate and compare the prevalence, abundance and accumulation of *T. crassus* in different age groups of whitefish *Coregonus lavaretus* L. s.l. and Arctic charr *Salvelinus umbla* (L.) of Achensee. Achleitner *et al.* (2009) showed that Arctic charr can also act as a primary second intermediate host; nevertheless, this study is the first to compare patterns of *T. crassus* infection in both fish species within a water body. Additionally we aimed to characterize the risk of *T. crassus* infection for *S. umbla* by analysing its feeding strategy during the occurrence of infected copepods. We also assessed whether or not the sympatric congener *T. nodulosus*, infects *C. lavaretus* and *S. umbla* in Lake Achensee.

Materials and methods

Study site

Lake Achensee (47°27'N, 11°42'E, 929 m above sea level, surface area = 6.8 km², z_{\max} = 133 m, z_{mean} = 67 m) is a holomictic prealpine lake situated in the Limestone Alps of North Tyrol in Austria (Beiwl & Mühlmann, 2008). The lake underwent eutrophication in the 1970s and 1980s,

but since 1991 total phosphorus concentration has been reduced to less than 3 µg l⁻¹, mainly due to sewage diversion (unpublished results). Hydropower generation causes water-level fluctuations of up to 6 m, and up to 11.5 m before 2004. Sixteen fish species currently exist in the lake (Gassner & Achleitner, 2006), including *S. umbla*, pike *Esox lucius* L., perch *Perca fluviatilis* L., and the commercially important *C. lavaretus*. Various stocking activities have been undertaken during the past decades, chiefly to enhance the angling experience (Kandler, fisheries manager of Lake Achensee, pers. comm., 2011).

Collection and examination of fish for *Triaenophorus*

Sampling of *C. lavaretus* and *S. umbla* was carried out 2–3 times a week between 25 May 2011 and 30 July 2011. Benthic and pelagic gillnets with mesh sizes from 10 to 43 mm (knot to knot) were deployed overnight at different locations and set at various depths. Additionally, nine *S. umbla* were obtained from recreational fishermen between June and July 2011. Fish were identified, measured to the nearest millimetre (total length), weighed (± 0.1 g) and their sex was determined. Subsequently livers of all fish and stomachs of *S. umbla* were fixed in 70% ethanol. In addition, alcohol was injected into each stomach to prevent further digestion. Fish were stored at 4°C for no more than 2 days before the number of parasites was ascertained.

The age of *C. lavaretus* was determined using scales sampled from the left body side between the dorsal fin and lateral line. The range of *S. umbla* age groups was estimated based on former length-at-age data for the Achensee population described by Gassner & Achleitner (2006). A total of 168 *C. lavaretus* and 120 *S. umbla* were investigated for the abundance (number of parasites per fish) of *T. crassus* plerocercoids. Each cooled specimen was skinned and detected plerocercoids were removed, excysted if they were not free, and counted. Starting on one side, a thin fillet of approximately 2 mm thickness was cut along the anterioposterior axis and the newly discovered plerocercoids were removed, excysted and counted. Cutting and investigating the fillets was continued, until all muscle tissue of one side was examined. Subsequently, the same procedure was applied on the other side. To ensure that no plerocercoid was counted twice, their scolices were used to determine the abundance. In the end, the fillets were cut into 5 mm stripes to reveal very small cysts that may have been overlooked. In addition to counting, the condition of *T. crassus* was categorized into intact and degenerated. Plerocercoids were classified as degenerated if they were shrunken, fragmented or their integuments started to lyse. Cysts were termed as degenerated, if they were empty, solid or contained only remains of plerocercoids. A random sample of about 200 plerocercoids located in the muscles of the hosts was fixed in 70% ethanol and studied under a light microscope at 200-fold to 400-fold magnification. Prevalence of *T. crassus* was determined with the same set of specimens that were used for estimating abundance. For *C. lavaretus*, an additional 54 individuals were investigated. Furthermore, livers of all specimens were studied for infection with *T. nodulosus*.

For this purpose the livers were cut into strips of approximately 2 mm thickness and examined.

In Achensee, *C. lavaretus* can be separated into a pelagic and a benthic morph. The pelagic whitefish represent the predominant portion of the whitefish stock and feed primarily on zooplankton, while the few benthic whitefish mainly feed on macrozoobenthos (Kandler, fisheries manager of Lake Achensee, pers. comm., 2011). The accumulation of *T. crassus* with fish age was studied by analysing 160 pelagic and 8 benthic whitefish specimens from 1 to 8 years in age. Benthic and pelagic whitefish of the same age were pooled, as the benthic specimens had similar *T. crassus* burdens as the pelagic ones. The newly incorporated plerocercoids of the season 2011 were not included in the fish-age-specific abundance of *T. crassus*. Thus, the reported abundance of plerocercoids reflects the state after the last *Triaenophorus* infection in 2010. As the investigation for the *T. crassus* abundance of *C. lavaretus* was performed during a period when most plerocercoids of 2011 were not yet developed or at an early stage of development, it was straightforward to separate them from plerocercoids of previous years. The annual *T. crassus* accumulation in *C. lavaretus* was computed by dividing the plerocercoid abundance by the number of times fish had been exposed to *T. crassus* invasions (Pulkinen & Valtonen, 1999). The number of annual invasions is indicated by fish age increased by one.

Dietary analysis of fish

The stomach samples of each month were pooled, as no remarkable differences were apparent between the different fish length classes. After the stomachs were opened, their total fullness was estimated visually on a percentage scale of 0% (empty) to 100% (full). Stomachs with no identifiable prey were excluded from further analyses, so that 68 remaining samples were investigated in detail. Prey were identified, counted and their numerical contribution (per cent abundance) to the diet was determined. The zooplankton items were identified to the species level and counted. If necessary, subsampling was applied. The other prey items were grouped into chironomids, other insects, fish and molluscs.

In order to assess the feeding strategy of *S. umbla*, a graphical analysis suggested by Amundsen *et al.* (1996) was used. Therefore, the prey specific abundance (P_i) was plotted against the frequency of occurrence (F_i) on a two-dimensional graph. The two indices can be described by the equations:

$$P_i = \left(\frac{\sum S_{iI}}{\sum \sum S_{ii}} \right) \times 100$$

$$F_i = N_i/N$$

where S_i is the number of prey i found in the stomach contents, S_{ii} is the total amount of food items found in only those predators with prey i in their stomachs, N_i is the number of predators with prey i in their stomachs, and N is the total amount of predators with food items in their stomachs (Amundsen *et al.*, 1996). The position of prey data points in the graph produced indicates the prey importance and provides insight into the feeding strategy

of the predator. A prey data point positioned in the upper left indicates that some individual predators are specialized on that particular prey. A prey data point located in the upper right, however, points out that the whole population is specialized on a given prey. Prey data points positioned in the lower part of the graph reflect a more generalistic feeding strategy. Points will be located in the lower right part of the graph if the corresponding prey are eaten occasionally by most predators. By contrast, points will be in the lower left if only a few predators sporadically consume the given prey. Amundsen *et al.* (1996) provide a more precise description of the method.

Data analysis

Mean length-at-age for the pelagic *C. lavaretus* was modelled using the von Bertalanffy growth model. Bootstrap methods were used to construct 95% confidence bounds and 95% prediction bounds for the model. Due to the small sample size, the growth of the benthic *C. lavaretus* was not modelled. The relationship between abundance of *T. crassus* plerocercoids and age of *C. lavaretus* was analysed with Spearman's rank correlation coefficient. Differences between age groups of *C. lavaretus* in annual accumulation of *T. crassus* were tested using a one-way analysis of variance (ANOVA; general linear model, 95% confidence). Data were tested for normal distribution and equal variance using the Kolmogorov–Smirnov test and the Levene's test, respectively. A Fisher's exact test was conducted to reveal differences in prevalence of *T. crassus* between *C. lavaretus* and *S. umbla*. For the test, the age groups were pooled within each species. The parasitological terminology of prevalence and abundance follows Bush *et al.* (1997).

Results

Infection levels of *Triaenophorus* in fish

All examined *C. lavaretus* were infected with *T. crassus* ($n = 222$). In *S. umbla*, however, only 15.8% of the investigated individuals harboured *T. crassus* ($n = 120$). The prevalence of this parasite differed significantly between the two species (Fisher's exact test: $df = 1$, $P < 0.001$). The congener *T. nodulosus* was not detected in *C. lavaretus* ($n = 222$) or *S. umbla* ($n = 120$). The mean length of examined pelagic *C. lavaretus* ranged from 174.6 mm (1-year-old fish) to 302.0 mm (8-year-old fish). Pelagic *C. lavaretus* showed rapid growth during the first 3 years of life, until they reached maturity at the age of 3+ (fig. 1). In *C. lavaretus* older than 3+, yearly length increments were small and growth was substantially reduced.

Mean abundance of *T. crassus* plerocercoids in *C. lavaretus* (pelagic and benthic morph pooled) significantly increased with fish age (fig. 2; Spearman $K_s = 0.74$, $df = 166$, $P < 0.001$). The increase was distinct in the range of age groups 0+ to 3+, while it levelled off in older fish. Fish belonging to the age group 2+ were already infected with 19.4 plerocercoids on average, while older specimens frequently harboured about 30 plerocercoids. The maximum individual infection with *T. crassus* consistently increased with fish age, until it culminated

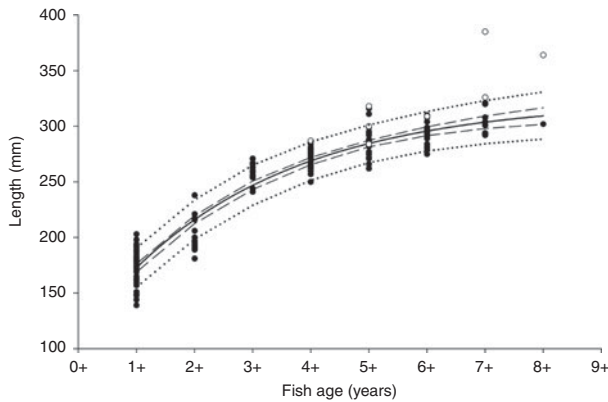


Fig. 1. Fish length/age values of pelagic (●) and benthic (○) *Coregonus lavaretus* from Lake Achensee during June/July 2011; the growth of pelagic fish was modelled using the von Bertalanffy growth model ($f = 323.5(1 - e^{-0.34(x - (-1.26))})$) and 95% confidence (---) and 95% prediction intervals (— · —) were computed using bootstrap methods.

at a maximum of 50 plerocercoids in the age groups 4+ and 5+. The mean annual accumulation of *T. crassus* plerocercoids (intake of plerocercoids per year) in *C. lavaretus* did not significantly differ between age groups (fig. 3; one-way ANOVA (GLM): $F = 1.65$, $df = 167$, $P = 0.125$). The mean accumulation in all age groups was 5.2 (SD = 2.2) plerocercoids per year. No increase of *T. crassus* with fish age or total length was apparent in *S. umbla*. The majority of infected fish harboured one or two parasites, while the maximum individual infection remained at a low level of three plerocercoids (table 1). The length of *S. umbla* ranged from 92.0 to 463.0 mm, which corresponded approximately to age groups 2+ and 9+.

In *C. lavaretus* a large proportion of *T. crassus* plerocercoids were encysted, whereas free (not encysted) plerocercoids were scarce (table 1). Overall, most plerocercoids were intact and only a small portion of them were degenerated. The former were frequently about 20 cm long, whereas the latter were much shorter, mainly encysted and often had a mushy appearance. Some degenerated cysts were yellowish, solid and contained only remains of plerocercoids. In infected *S. umbla*, however, both intact and degenerated plerocercoids were of the same size and rarely exceeded 12 cm. Moreover, degenerated specimens made up more than half of all harboured plerocercoids in *S. umbla* (table 1). In contrast to *C. lavaretus*, the vast majority of degenerated plerocercoids were not encysted.

Feeding strategy of fish

No major differences in the diet between length classes of *S. umbla* were detected in June and July. On the other hand, the proportion (per cent abundance) of food items in *S. umbla* varied strongly over time (table 2). Chironomids, mainly pupae, dominated the diet in June and became rare in July. *Bosmina* sp. was the most consumed zooplankton species in June, whereas *Daphnia* sp. made up more than 90% of the entire diet in July.

Cyclops sp. was completely missing from the stomach content in June and not very abundant in July. Likewise *Cyclops*, fish, molluscs and insects (excluding chironomids) were not frequent in the diet of *S. umbla*. It is likely that oligochaetes were not detected because they are digested rapidly. The feeding strategy graphs (fig. 4) reveal a specialization at the population level of *S. umbla* in both June and July. This population specialization was reflected by one prey point for each month positioned in the upper right part of the diagram. The population specialized on chironomids and *Daphnia* sp. in June and July, respectively. The other food items, including *Cyclops* sp., with their prey points in the lower left part, were only eaten occasionally at a predominantly individual level. Besides the specialization at the population level, a slight individual feeding specialization on *Bosmina* sp. existed in June.

Discussion

One of the main goals of the present study was to investigate the pattern of *T. crassus* infection in *C. lavaretus* and *S. umbla* of Achensee. Both fish species are known to be second intermediate hosts for *T. crassus* (Miller, 1945b; Kuperman, 1981; Pulkkinen & Valtonen, 1999; Achleitner et al., 2009). *Coregonus lavaretus* of Achensee exhibited extremely heavy *T. crassus* burdens. The prevalence of *T. crassus* plerocercoids was 100% in all examined age groups. Such a high prevalence has only been recorded for older age groups, while in fish aged 0+ and 1+ the prevalence never exceeded 45% (Miller, 1945b; Petersson, 1971; Amundsen & Kristoffersen, 1990; Pulkkinen & Valtonen, 1999). The high prevalence of *T. crassus* in younger *C. lavaretus* of Achensee is, therefore, exceptional. The high burden of *T. crassus* is also reflected in a remarkably high load of plerocercoids in all age groups. The mean abundance of *T. crassus* in *C. lavaretus* significantly increased with fish age, which is in line with the results of other studies (Petersson, 1971;

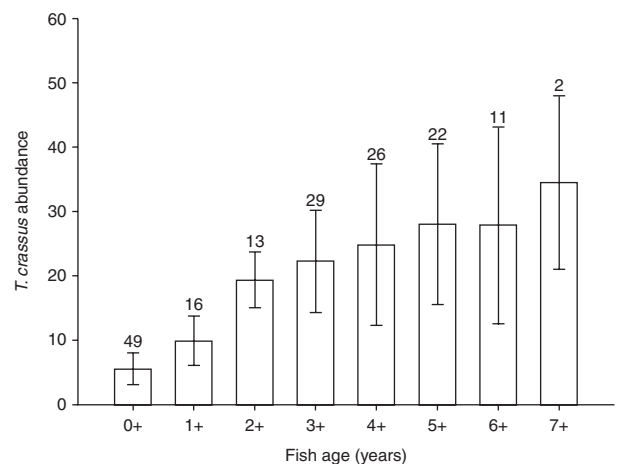


Fig. 2. Mean abundance values (\pm SD) of *Trianaophorus crassus* in *Coregonus lavaretus* from Lake Achensee, relative to fish age. Numbers of fish studied within each age group are indicated above the bars.

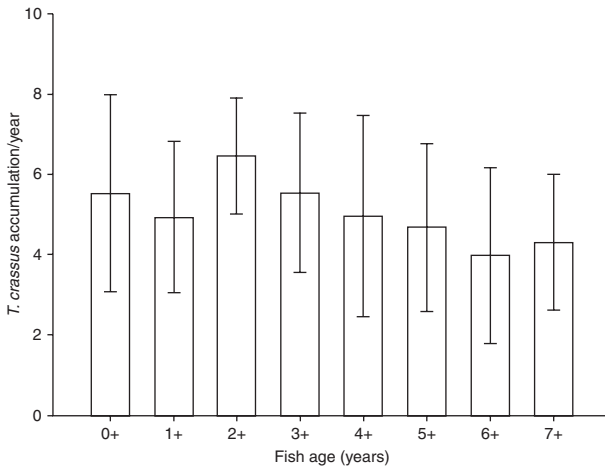


Fig. 3. Mean annual accumulation of *T. crassus* plerocercoids (\pm SD) for the age groups of *Coregonus lavaretus* from Lake Achensee. The numbers of investigated fish are as in fig. 2.

Pulkkinen & Valtonen, 1999). However, we showed much higher fish-age-specific abundances of *T. crassus* than reported in previous work. Dick & Rosen (1982) observed that young-of-the-year whitefish contained one or two plerocercoids and the mean abundance of *T. crassus* for 1- to 4-year-old whitefish was described to be in the range of 0–8 plerocercoids (Miller, 1945b; Pulkkinen *et al.*, 1999). In Achensee, however, 0+ aged whitefish already harboured 5.5 *T. crassus* on average. The mean abundance rapidly increased to 19.4 plerocercoids per fish in the age group 2+ and reached more than 27 plerocercoids in older fish. Pulkkinen & Valtonen (1999) noticed such high loads of *T. crassus* only in whitefish aged 6 years and older, whereas mean abundances in 1- to 5-year-old fish in their samples stayed below nine plerocercoids.

This mass infection of *T. crassus* may be the result of several factors. First, the immune defence of *C. lavaretus* against this parasite seems to be weak in Achensee. According to Pulkkinen & Valtonen (1999), the annual accumulation of *T. crassus* in whitefish of Lake Puruvesi remained at a low level for young age groups, until the intake of parasites almost doubled in older age groups. One possible explanation for the increased accumulation is a breakdown of immune defence, once a critical number of parasites per fish is exceeded (Pulkkinen & Valtonen, 1999). In contrast, the intake of *T. crassus* in *C. lavaretus* of Achensee constantly remained at a very

high level throughout all age groups, underscoring a potentially weak immune defence. However, an experimental infection study would have been needed to clarify this claim, as it is unknown how many infected copepods had been consumed by the fish and, therefore, the efficiency of the immune defence cannot be rated.

Second, the ultra-oligotrophic conditions of Lake Achensee very likely contribute to the high burdens of *T. crassus*. It is known that the transmission of *Triaenophorus* sp. increases in water bodies with low nutrient concentrations because of the relative dominance of (infected) copepods compared to cladocerans (Watson & Lawler, 1965; Molzen, 2005). Furthermore, the zooplankton biomass is low in oligotrophic lakes, so that planktivorous fish have to prey additionally on copepods beside the preferred cladocerans to meet their energy demands (Watson & Lawler, 1965; Kuperman, 1981; Molzen, 2005; Brinker & Hamers, 2007).

Third, the mass infection of *T. crassus* may be related partly to the water-level fluctuations in Achensee. Petersson (1971) highlighted that in lakes with artificial water-level fluctuations both pelagic and benthic whitefish species had a high infection with *T. crassus*, although the macrozoobenthos-dominated diet of the benthic species should have counteracted a high invasion. He argued that the altered environment of regulated lakes favours especially benthic whitefish to evolve a pronounced planktivorous feeding habit and thus increases the infection with *T. crassus*. In fact, pelagic and benthic *C. lavaretus* of Achensee had similar *T. crassus* burdens, which reinforces the argument of Petersson (1971) that water-level fluctuations may favour a shift from benthic to planktonic feeding behaviour. Nevertheless, Gassner & Achleitner (2006) and our own observations in 2011 illustrate that the vast majority of *C. lavaretus* in Achensee reside in the pelagic zone and thus mainly utilize crustacean zooplankton (Schulz, 1979; Anegg *et al.*, 2014). It remains unclear to what extent the water-level fluctuations enhance the degree of plankton feeding and the risk of *T. crassus* infection. Moreover, it is reasonable to assume that *E. lucius* in Achensee, as definitive hosts, are co-responsible for the high *T. crassus* burdens in *C. lavaretus*. In fact, it seems that over the past few decades the population has increased (Kandler, fisheries manager of Lake Achensee, pers. comm., 2011; authors' observations, 2011) which facilitates the transmission of the parasite.

In *S. umbla* the prevalence of *T. crassus* plerocercoids was significantly lower than in *C. lavaretus*. Less than 16% of *S. umbla* were infected and most infected fish only

Table 1. The frequency of occurrence (%) of plerocercoids of *Triaenophorus crassus* as encysted or free and intact or degenerated in 168 *Coregonus lavaretus* and 120 *Salvelinus umbla* from Lake Achensee in June/July 2011.

	Maximum number of <i>T. crassus</i> in one fish	Plerocercoids of <i>T. crassus</i>			
		Encysted		Free	
		Intact	Degenerated	Intact	Degenerated
<i>Coregonus lavaretus</i>	50	83.89	0.70	15.37	0.03
<i>Salvelinus umbla</i>	3	11.54	7.69	30.77	50.00

Table 2. The proportion of food contents (%) in the stomach of 40 (June) and 28 (July) *S. umbla* from Lake Achensee.

Food contents (%)	June	July
Insects		
Chironomids	85.57	0.56
Other insects	2.77	0.04
Crustaceans		
<i>Bosmina</i>	8.03	1.05
<i>Daphnia</i>	2.11	92.36
<i>Cyclops</i>	0.00	5.92
Molluscs	1.25	0.00
Fish	0.27	0.06

harboured one or two plerocercoids. Furthermore, no increase of *T. crassus* with fish age or total length was apparent. These findings are quite surprising in the light of the high burdens of *T. crassus* in *C. lavaretus*, especially because Achleitner *et al.* (2009) documented a mass infection of *T. crassus* in *S. umbla* of Lake Grundlsee, another Austrian lake. Both fish species are vulnerable to infection with *T. crassus* and, although the parasite is heavily represented in Lake Achensee, *S. umbla* is only marginally infected. Infection with *T. crassus* plerocercoids requires a trophic relationship between the two intermediate hosts. Due to the strong dietary plasticity of Arctic charr (Hofer & Medgyesy, 1997; Amundsen *et al.*, 2008; Eloranta *et al.*, 2010, 2011) trophic interactions can vary strongly between and within populations. Some populations exert a pronounced preference for crustacean zooplankton, which implicates a higher risk for infections with copepod-transmitted parasites (Bérubé & Curtis, 1986; Knudsen *et al.*, 2008, 2010), particularly as some Arctic charr populations or individuals specialize on copepods (Dahl-Hansen *et al.*, 1994; Knudsen *et al.*, 1996).

In order to assess the risk of *T. crassus* infection for *S. umbla* in Achensee, their feeding strategy was studied

in June and July. This time slot was selected because in Achensee copepods are infected by *Triaenophorus* spp. between June and the beginning of August (Anegg *et al.*, 2014). The detected proceroids in August were most likely *T. nodulosus* (with respect to the findings of Miller (1945a), Lahnsteiner *et al.* (2009) and Sichrowsky *et al.* (2013)). Copepods were completely missing from the stomach contents of *S. umbla* in June. In July, only a small amount of copepods, in particular *Cyclops* sp., was consumed by a few individuals, while the vast majority of the population specialized on *Daphnia* sp. Thus, it can be suggested that the feeding habit of the population is probably a major cause for their marginal infection with *T. crassus*. Although the diet of *S. umbla* was only studied during one period of *T. crassus* transmission, there is evidence that copepods were also avoided in other years (unpublished results). This is congruent with Knudsen *et al.* (1996), whose findings indicate that Arctic charr maintain dietary specializations over years. Besides feeding strategy, habitat choice of the *S. umbla* population may protect this species from high infection with *T. crassus*. According to Watson & Lawler (1965), copepods infected with *Triaenophorus* spp. are most abundant in shallow waters near the shore. *Salvelinus umbla* of Achensee, however, primarily inhabits the benthal area of the deep-water zone (Gassner & Achleitner, 2006; authors' observations, 2011).

Apart from the low *T. crassus* infection in *S. umbla*, the high rate of degenerated plerocercoids is noteworthy. More than half of all harboured plerocercoids in *S. umbla* were degenerated, whereas in *C. lavaretus* more than 99% of the plerocercoids were intact. It appears that *T. crassus* is disturbed in its development in *S. umbla*, as many young plerocercoids began to degenerate before they were encysted. One possible explanation for the low infectivity of *T. crassus* for *S. umbla* in Achensee could be a high host specificity of the local parasite population for *C. lavaretus* and not for *S. umbla*. Pulkkinen *et al.* (1999) confirmed that the host specificity of this parasite can

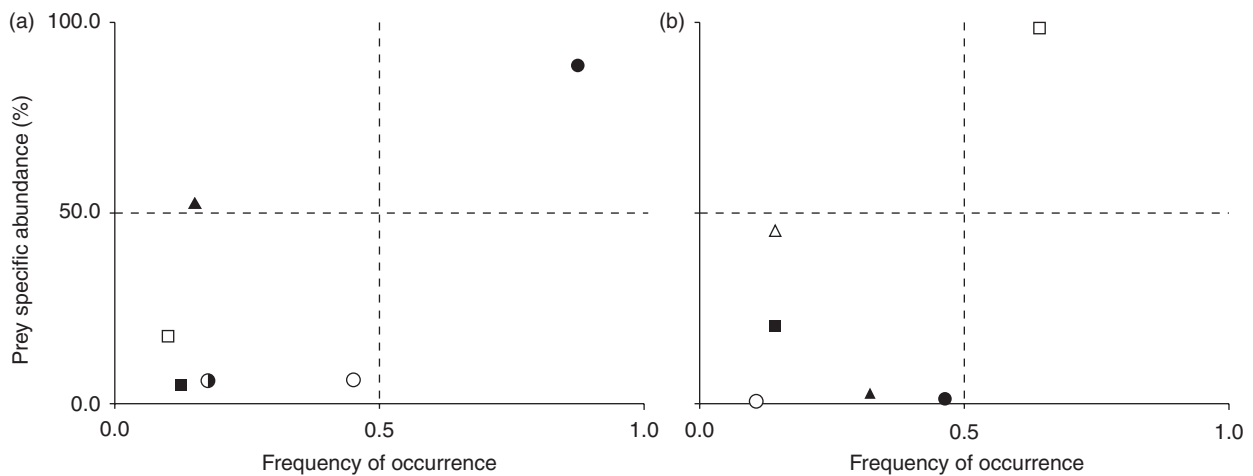


Fig. 4. Prey specific abundance (%) against the frequency of occurrence within the stomach of (a) 40 *Salvelinus umbla* in June and (b) 28 *S. umbla* in July 2011 from Lake Achensee; *Bosmina* sp. (▲), *Cyclops* sp. (△), fish (■), *Daphnia* sp. (□), chironomids (●), other insects (○) and molluscs (◐).

vary even locally between *Coregonus* species. Another reason might be an effective immune defence of the *S. umbla* population against this parasite.

In conclusion, this study demonstrates that a remarkably high prevalence and abundance of *T. crassus* in *C. lavaretus* already occurs in younger age groups. In contrast, previous studies have merely revealed high burdens of *T. crassus* in older age groups (Miller, 1945b; Dick & Rosen, 1982; Amundsen & Kristoffersen, 1990; Pulkkinen & Valtonen, 1999). Even though *C. lavaretus* exhibited an exceptionally high *T. crassus* infection status, the *S. umbla* population of Achensee was marginally infected. With respect to the mass infection of *S. umbla* in another Austrian lake (Achleitner et al., 2009), the present results corroborate the great variability in the pattern of *T. crassus* infection. Thus, one should be particularly cautious in generalizing infection characteristics of this parasite without detailed investigations. Based upon our findings, we recommend reducing the amount of older *C. lavaretus* in Achensee. These age groups have an extremely high abundance of *T. crassus* plerocercoids, hence they pose a high risk for transmission of this parasite to *Esox lucius*, the definitive host. Simultaneously, a strong decimation of pike will be required to reduce the *Triaenophorus* spp. populations (Amundsen & Kristoffersen, 1990; Achleitner et al., 2009). Future research should study in depth the effects of such high *T. crassus* burdens on growth, behaviour and survival of second intermediate hosts under natural conditions.

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Conflict of interest

None.

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