

Long-term population dynamics of *Diphyllobothrium ditremum* and *D. dendriticum* (Cestoda: Pseudophyllidea) in their salmonid hosts following a fish removal experiment

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Summary

Parasite-host interactions are important in understanding ecosystem processes, for instance by using trophically transmitted parasites as indicators of host ecology. Parasite infections are expected to correlate with host density, habitat choice and feeding behaviour. The importance of long-term data and perturbation experiments has been emphasized for advancing our knowledge of the parasite-host relationship. Over a five-year period in the 1980s a mass removal of fish was implemented on a stunted population of Arctic charr (*Salvelinus alpinus* (L.)) in subarctic lake Takvatn. This culling of fish can be seen as a large ecological experiment, and the effects have been monitored with long-term analysis on the fish populations of the lake. Here, I study the long-term effects of this fish removal experiment on two component populations of the tapeworms *Diphyllobothrium ditremum* and *D. dendriticum* infecting Arctic charr. Infections are also compared between charr and brown trout (*Salmo trutta* (L.)). The infections of both *Diphyllobothrium* species in Arctic charr decreased after the fish removal, reflecting a shift in habitat and diet from pelagic zooplanktivory to littoral benthivory in the charr population, and a reduced abundance of copepods in the zooplankton community. The decrease was more drastic in the *D. dendriticum* population suggesting altered transmission rates to the avian final hosts. Infections of both parasite species oscillated between years, likely as a result of cycles in the population density of three-spined stickleback (*Gasterosteus aculeatus* (L.)). Arctic charr had higher infections of *D. ditremum* than brown trout, while the opposite was true for *D. dendriticum* infections. This suggests niche segregation between the two fish species with charr grazing more on zooplankton and trout more on fish, as *D. dendriticum* has been described as an indicator of piscivory. The study has highlighted how parasite infections respond to a large perturbation, and how sensitive they are to variation in ecological processes.

Introduction

Parasite-host interactions are key in understanding ecosystem processes (Marcogliese and Cone 1997, Hudson et al. 2006, Lafferty et al. 2008a), for instance in respect to how parasite-mediated effects may alter the flow of energy through ecosystems (Hudson et al. 2006), or by using parasites as biological indicators to provide information on various aspects of their host's biology (Williams et al. 1992). Parasites can also be used as indicators for the trophic links between host species (Marcogliese and Cone 1997), and ecological differences between competitors at the same trophic level can be assessed by analysing their trophically transmitted parasite faunas (Knudsen et al. 2008). Marcogliese (2004) phrases it nicely when he states that parasites are small players with crucial roles in the ecological theatre. Most people, however, have negative associations to parasites (Hatcher et al. 2012), and the presence of certain parasites in populations subjected to human harvest is a problem in several animal taxa (e.g. Kuris and Lafferty 1992, Barnes et al. 1995, Chai et al. 2005). Here, I address the long-term effects of a mass removal of fish as an effort to reduce parasite burdens in a highly parasitized population of Arctic charr (*Salvelinus alpinus* (L.)). Anderson (1991) emphasized the importance of long-term data and perturbation experiments in testing ecological ideas regarding the parasite-host relationship, and the mass removal of charr can in this respect be seen as a large-scale ecological experiment monitored over decades.

Aquatic habitats have physical and ecological properties that make these systems optimal for the maintenance and evolution of parasite life cycles (Barber et al. 2000). The trophic position of teleost fishes puts them in an ideal position as hosts for parasitic organisms (Barber et al. 2000). Fish serve as hosts for many species of helminth parasites (see Marcogliese 1995). Several helminths, including tapeworms, have relatively long lifespans in relation to that of their fish hosts (Anderson & Gordon 1982). The infrapopulations of such parasites are therefore to a large extent controlled through immigration, while the metapopulation is controlled by average infection rates and the death of hosts (Anderson and Gordon 1982). Helminth parasites normally possess complex life cycles where they are trophically transmitted from one host to another by consumption of infected hosts (Amundsen et al. 2003).

Such trophically transmitted parasites tend to exhibit more aggregated (or over-dispersed) distributions within the host population compared to parasites with other types of life cycles (Shaw and Dobson 1995, Lester 2012). These aggregations can be caused by multiple factors such as heterogeneity in habitat use or feeding behaviour within the host population (Knudsen et al. 2004, 2008), individual differences in immunological defences against the parasite (Anderson and Gordon 1982, Morrill and Forbes 2012), and/or aggregated distributions of infective stages through space and time (Anderson and Gordon 1982, and references therein).

One group of trophically transmitted tapeworms, which are commonly found and widely distributed in freshwater fish, especially salmonids, is the *Diphyllobothrium* genus (Henricson 1977). In Scandinavia, two common species of *Diphyllobothrium* using salmonids as second intermediate host, are *D. dendriticum* (Nitzsh) and *D. ditremum* (Creplin) (Henricson 1977). Both utilize copepods as first intermediate hosts and may, in addition to salmonids, utilize 3-spined stickleback (*Gasterosteus aculeatus*) and burbot (*Lota lota*) as their second intermediate hosts (Vik 1964, Halvorsen 1970). The parasites can also be transmitted from fish to fish through piscivory (Vik 1964). The only stage where their hosts differ is as adults where they utilize different avian and (to a lesser extent) mammalian final hosts (Vik 1964, Halvorsen 1970).

Two fish species that frequently serve as hosts for *Diphyllobothrium* spp. are brown trout (*Salmo trutta* (L.)) and Arctic charr. These salmonids occur commonly throughout Scandinavia (Klemetsen et al. 2003). Lake resident populations utilize similar niches in allopatry, with both species preferring benthic prey in the littoral zone (Nilsson 1963). The brown trout is however a more efficient benthivore, and is more aggressive and more territorial than the Arctic charr (Nilsson 1963, Jansen et al. 2002). Hence, in sympatry, the Arctic charr appears to be excluded from the littoral areas of the lake during summer and autumn, while brown trout feeds similarly as in allopatry (Nilsson 1963, Langeland et al. 1991). This sympatric niche segregation may also be reflected in the parasite communities of the two salmonids. Knudsen et al. (2008) found that Arctic charr harboured more copepod-transmitted parasites than brown trout, and related this to charr feeding more upon zooplankton.

The ecological interactions between *Diphyllbothrium* spp. and their second intermediate fish hosts have been studied extensively since the middle of the 20th century (Hickey and Harris 1947, Henricson 1977, Halvorsen and Andersen 1984, Sharp et al. 1992, Kristoffersen 1993). The plerocercoids in the fish can live several years in their host, which therefore can accumulate high infections (Henricson 1977, Halvorsen and Andersen 1984). Many studies addressing these two parasites in sympatry, have shown that the prevalence and mean abundance of *D. ditremum* is higher than that of *D. dendriticum* (e.g. Henricson 1977, Knudsen et al. 1997). However, piscivorous fish may harbour more *D. dendriticum* relative to *D. ditremum*, as the plerocercoids of *D. dendriticum* are shown to survive piscivory better (Halvorsen & Wissler 1973). Three-spined sticklebacks are shown to be important transmitters of *D. dendriticum* to piscivorous trout (Vik 1957).

Differences in the density and habitat use of fish populations have been shown to influence the structure of their invertebrate prey communities (Klemetsen et al. 2002), which could in turn affect the fauna of trophically transmitted parasites in the fish. Stunted growth is a common problem in populations of Arctic charr (Amundsen et al. 1993), and lakes that are easily accessible for humans often contain populations of stunted small-sized fish as the larger individuals have been selectively removed with large-meshed gill nets (Klemetsen et al. 2002). Such populations of small-sized fish are of little commercial value (Ylikarjula et al. 1999), and may exhibit high infections of certain parasites, especially tapeworms that utilize planktonic copepods as intermediate hosts (Kennedy et al. 2001, Amundsen et al. 2002). Reducing the number of fish in stunted populations has been suggested as a method of improving their status related to growth rates and condition (Amundsen et al. 1993). In the early 1980s, Lake Takvatn in Northern Norway contained a stunted Arctic charr population, characterized by poor growth and high infections of plerocercoids of the tapeworms *D. ditremum* and *D. dendriticum* (Kristoffersen 1986). A large fish removal experiment was carried out with two main management goals; to increase the growth of the Arctic charr, and to reduce its parasite burdens (A. Klemetsen pers. comm.). Scientifically, this whole-lake perturbation constitutes a large-scale ecological experiment addressing population and community dynamics and trophic interactions in a subarctic freshwater ecosystem, and the effects have been followed up by long-

term studies carried out since 1980 (see e.g. Klemetsen et al. 2002, Amundsen et al. 2007, Persson et al. 2007).

The long-term analyses of the Arctic charr population following the fish removal experiment showed an increase in somatic growth and size, an effect that has been sustained over time (Klemetsen et al. 2002; Amundsen et al. 2007). Three years after the end of the experiment, brown trout had increased in numbers after being nearly absent prior to the perturbation (Klemetsen et al. 2002), and the importance of this species has increased over the following decades (Persson et al. 2007, Eloranta et al. 2013, P.-A. Amundsen, unpublished data). The present study addresses the long-term variation in the infection of plerocercoids of *D. ditremum* and *D. dendriticum* in Arctic charr in the years prior to, during and following the fish removal experiment. Data on plerocercoids in brown trout after its reappearance are also included. The study covers a total period of 31 years, mostly with annual sampling, and these time-series data have been used to address three main questions: Firstly, how does a mass removal of fish affect the infections of the two *Diphyllbothrium* species in a highly parasitized population of Arctic charr? Secondly, do the two species show similar temporal trends in abundance? Finally, are there differences in the *Diphyllbothrium* infections between Arctic charr and brown trout in terms of prevalence, mean intensities and the relative incidence of the two parasite species?

Large ecological changes have occurred in the lake system after the fish removal experiment was implemented. The zooplankton community has shifted from being dominated by copepods, to inhabiting larger cladoceran species (Dahl-Hansen 1995; P.-A. Amundsen et al., unpublished data). Simultaneously, the availability of benthic prey has increased, resulting in a habitat shift in Arctic charr, with young fish less frequently utilizing the pelagic and profundal areas (see Klemetsen et al. 2002). Consequently, the diet of Arctic charr shifted, with an increase in the importance of invertebrate benthic prey (Amundsen et al. 1993) The three-spined stickleback population in Takvatn are efficient zooplankton feeders (Dahl-Hansen 1998), and also constitutes an important part of the diets of the salmonids in the lake (Amundsen 1994, Klemetsen et al. 2002). Furthermore, following the stock reduction experiment, the predation on juvenile charr has increased both through cannibalism (Amundsen 1994, Klemetsen et al. 2002) and piscivory from the increasing brown trout

population (Klemetsen et al. 2002, Persson et al. 2007). Based on the background described above, it was hypothesized that i) the *Diphyllbothrium* infections of Arctic charr have decreased after the stock removal experiment through a reduction in the density of hosts and reduced predation on copepods, and ii) piscivorous fish may aggregate large infections, especially of *D. dendriticum*, due to secondary establishment of plerocercoids from their prey fish, and iii) Arctic charr have higher *Diphyllbothrium* infections than brown trout, as Arctic charr typically feed more on zooplankton. Finally, iv) it was hypothesised that the relative infections of the two *Diphyllbothrium* species are different between the two fish species, with Arctic charr mostly harbouring *D. ditremum*, and brown trout having higher intensities of *D. dendriticum*, being a more prominent piscivorous species.

Material and methods

Study site

Takvatn is a 14,2 km² large and 80 m deep dimictic lake located in the Målselv River system in Troms county, Northern Norway. It is situated 214 meters above sea level, and is typically ice-covered from November to early June each year (Amundsen et al. 2007, 2009). The lake is oligotrophic with Secchi depths ranging between 14 and 17 m, and phosphorous levels not exceeding 5 µg L⁻¹ (Eloranta et al. 2013). The landscape surrounding the lake is dominated by birch (*Betula pubescens*) with some pine trees (*Pinus sylvestris*) and patches of farmland (Amundsen et al. 2007, 2009).

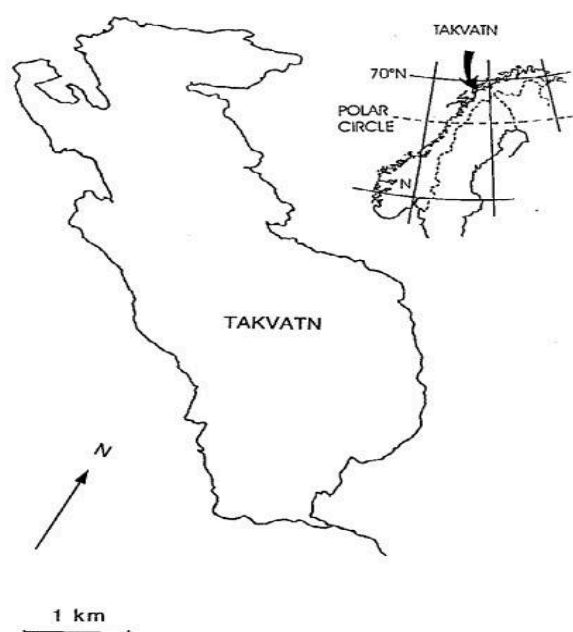


Fig. 1. Map of Takvatn, including the location of Takvatn in Norway.

Fish community

Brown trout is the only native fish species in Takvatn. The population was overharvested in the early 1900s, and Arctic charr was introduced to the lake around 1930 (Persson et al. 2007). In the years following the introduction, the Arctic charr grew large and was considered a good food resource by local fishermen (Amundsen et al. 1993). After some years the population became dense, with declining growth rates and smaller sizes. 3-spined stickleback (*Gasterosteus aculeatus*) was introduced to the lake around 1950 as a potential prey fish for brown trout and Arctic charr. By 1980, the fish community in Takvatn was dominated by a very dense population of stunted

Arctic charr (Amundsen & Klemetsen 1988), with sticklebacks also being highly numerous and brown trout nearly absent from the lake (Amundsen et al. 1993).

Fish removal programme

From 1984 to 1989, a total of 666 000 or 31,3 metric tons of Arctic charr were removed from the lake by intensive fishing with baited funnel traps. This was conducted as volunteer work by landowners and members of local fishing associations (Amundsen et al. 1993). During and following this perturbation, the density of Arctic charr decreased while the brown trout population increased (see fig. 2).

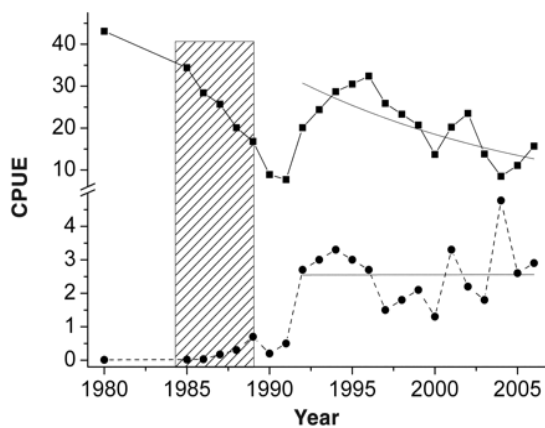


Fig. 2. Changes in the abundance of charr (squares, solid lines) and brown trout (circles, dashed lines) in Takvatn between 1984 and 2006. Hatched area shows period of fish removal programme. From Persson et al. (2007).

Bird community

The bird community of Takvatn is dominated by fish-eating birds, namely red-breasted mergansers (*Mergus serrator*) and common gulls (*Larus canus*), with Arctic terns (*Sterna paradisaea*) being abundant some years (Klemetsen and Knudsen 2013). Tufted ducks (*Aythya fuligula*), common scoters (*Melanitta nigra*) and black-throated divers (*Gavia arctica*) are also regularly breeding at the lake (Klemetsen and Knudsen 2013). Of these species, red-breasted mergansers and black-throated divers are the most important final hosts for *D. ditremum*, while common gulls are final hosts for *D. dendriticum* (Halvorsen 1970).

Fish sampling

Fish used in the present study were collected in the years 1980, 1981, 1987, 1988 and every year between 1992 and 2011 except in 1998 and 2000. The fish were sampled throughout the ice-free season using bottom and floating gill nets. Net series with bar mesh sizes from 10 to 52 mm knot to knot were used prior to 1989. From 1989 and onwards, multi-mesh nets with panels ranging from 10 to 45 mm knot to knot were used (Klemetsen et al. 2002). The nets were left overnight for approx. 12 hours in the lake. Fish were collected from the littoral (< 15 m depth), profundal (25 – 40 m depth) and pelagic (offshore, 0 – 6 m depth) zones of the lake. In the field, the fish were weighed, measured in fork length, and sex and gonad maturation were recorded. Otoliths were taken from each fish and preserved in ethanol. In the laboratory, age was determined by immersing the otoliths in glycerol, and counting the growth seasons using a dissecting microscope (Klemetsen et al. 2002). An overview of the fish used in the present study is provided in table 1.

Table 1. Sample sizes and mean age and length of Arctic charr and brown trout sampled for *Diphyllobothrium* spp. screening.

Year	N Arctic Charr	Mean Age (± SD)	Mean Length (± SD)	N brown trout	Mean Age (± SD)	Mean Length (± SD)
1980	487	5.8 (2.3)	170.8 (28.3)	-	-	-
1981	179	6.5 (2.1)	179.4 (28.1)	-	-	-
1987	516	4.5 (2.0)	173.1 (53.3)	-	-	-
1988	244	5.2 (2.2)	191.0 (64.9)	-	-	-
1992	311	6.3 (3.3)	228.2 (104.6)	-	-	-
1993	56	7.9 (3.1)	283.8 (89.9)	-	-	-
1994	240	5.0 (2.9)	194.4 (86.0)	-	-	-
1995	170	3.5 (1.8)	213.9 (58.4)	-	-	-
1996	115	4.0 (1.3)	227.2 (34.5)	-	-	-
1997	95	3.9 (1.7)	210.8 (64.5)	-	-	-
1999	150	5.8 (1.6)	233.4 (73.9)	-	-	-
2001	62	5.3 (2.1)	210.8 (87.0)	11	4.9 (2.0)	256.5 (68.4)
2002	75	4.2 (1.8)	178.4 (52.3)	24	4.6 (1.6)	244.5 (65.6)
2003	77	4.2 (1.8)	177.8 (56.4)	6	5.7 (0.9)	340.8 (70.5)
2004	60	4.2 (1.9)	179.8 (61.1)	48	3.8 (1.5)	240.8 (76.7)
2005	67	4.7 (2.1)	211.4 (88.8)	36	3.8 (1.4)	234.6 (84.0)
2006	72	4.5 (1.9)	180.9 (67.0)	44	3.8 (1.7)	220.0 (95.8)
2007	58	4.5 (1.9)	171.6 (52.7)	37	3.6 (1.2)	213.8 (81.0)
2008	61	5.4 (2.6)	220.9 (83.1)	13	4.3 (1.1)	258.3 (51.1)
2009	82	3.8 (1.3)	175.4 (51.3)	18	4.5 (1.7)	228.1 (79.2)
2010	92	5.5 (2.3)	253.3 (82.9)	68	4.5 (1.7)	249.8 (113.5)
2011	61	4.4 (1.8)	200.4 (72.8)	64	4.2 (1.4)	210.8 (89.8)

Parasite sampling

In the field cysts of *Diphyllobothrium* spp. located on the stomach wall, visceral organs and flesh of each dissected fish were placed in digestive fluid (1 L containing 2 ml HCl, 5 g pepsin, 9 g NaCl and water) to excyst the plerocercoids (Knudsen and Klemetsen 1994). The excysted plerocercoids were stored on buffered 4% formalin and later identified to species in the laboratory as described by Andersen and Gibson (1989). The most important morphological features that distinguish the two *Diphyllobothrium* species are size, scolex morphology and the shape and appearance of the body. *Diphyllobothrium ditremum* are less than 2,5 cm, their scolex is extruded and they have a smooth body surface that lack any sign of segmentation. *Diphyllobothrium dendriticum* can be longer than 10 cm, their scolex is partly retracted and they have a wrinkled body surface that appears segmented. The overall body shape of *D. dendriticum* appears more rectangular while *D. ditremum* is more oval. These features are less prominent in the smallest individuals (Halvorsen 1970), which could lead to erroneous identifications. The extent of misidentifications is however thought to be small, and should not be biased toward one species (Kristoffersen 1986).

Statistical analyses

Statistical parameters

The terms prevalence, mean abundance and mean intensity are used according to Bush et al. (1997). Prevalence (P) is the frequency or percentage of a particular host population that is infected with a particular parasite species. It is calculated by dividing the number of hosts infected with a particular parasite species, a, by the total number of hosts examined for that parasite, N.

$$P = a / N \times 100$$

Mean abundance (A) is the average number of a particular parasite species among all members of a particular host population. It is calculated as the total number of individuals of the parasite within the sample of hosts b, divided by N.

$$A = b / N$$

Mean intensity (I) it is the average intensity of a particular species of parasite among the infected members of a particular host species. It is calculated similarly to mean abundance, but here b is divided by the number of examined hosts that are infected with the parasite, n.

$$I = b / n$$

To adjust for differences in host body size among sampling years, intensity per 100 gram was calculated among infected individuals. The mean intensity/100 gram fish is presented as relative intensity (RI) and calculated as

$$RI = \sum [\text{intensity} / \text{weight (g)} \times 100] / n$$

Temporal analyses

The temporal analyses of prevalence for each year are presented longitudinally with fitted regression lines. The linear regressions were performed for both parasite species, providing the slope for prevalence with increasing sampling years. This tells us if there is an increasing or decreasing trend in prevalence from 1980 and onwards, and provides a p-value which is the probability of the observed values being obtained if the null hypothesis (i.e. no difference) is true. A separate linear regression including an interaction between the two species was performed to check if they differed temporally in prevalence. A regression analysis assumes that the residuals are constant, independent and follow a normal distribution. The validity of these assumptions was tested using a diagnostic tool plot in R, and regressions where the residuals did not meet these terms were omitted from the results. The same method was used for analysing temporal variations in mean abundance and mean intensity. In this case the average for each year was based upon count data from individual fish (i.e. intensities). The linear regression for relative intensity was performed on log-transformed values to meet the model assumptions. The dispersion of parasites tends to be aggregated, with high variance to mean ratios ($s^2 / \bar{x} > 1$) (Wilson et al. 2002). Such over-dispersed data are often assumed to follow a negative binomial distribution. Negative binomial distributions do not allow for regular confidence intervals to be made, and variation is thus presented by standard errors (table 3).

Comparisons of Diphyllbothrium infections in Arctic charr and brown trout

For comparing the infections of the two *Diphyllbothrium* species in Arctic charr and brown trout, data from 2001 to 2011 were pooled together to get a large sample size and thus provide a general picture of the infections regardless of yearly differences. The prevalence of infection is compared between the two fish species using a chi-squared test. This test analyses the probability that the observed counts of infected and uninfected brown trout and Arctic charr are independent of one another. To test for differences in intensities (of *D. ditremum* and *D. dendriticum*) between trout and charr, a two-tailed permutation (or randomization) test was done/used/employed. This test pools all the data from the sampling groups (both uninfected and infected individuals) and reassigns it without replacement to the to the treatment levels, keeping the number of observations identical as in the original data (Crowley 1992). This was simulated 100 000 times, and the p-value is the proportion of all simulations yielding test statistics at least as extreme as the observed value. Permutation tests do not assume any underlying distribution in the data, and are not very sensitive to outliers (Crowley 1992). A separate test was conducted for each *Diphyllbothrium* species.

A generalized linear model (GLM) was used to do a negative binomial regression for estimating the mean intensities of the two parasite species in relation to fish length. Wilson and Grenfell (1997) encouraged the use of GLMs for interpreting parasitological data. As the data is over-dispersed with variance/mean ratios exceeding 1, a negative binomial parameter, *theta*, is included in the GLM as a measure of aggregation. Separate GLMs were conducted for each parasite species with fish length and species (Arctic charr and brown trout) as predictor variables and mean intensity of infection as the response variable. The model output gives the intercept value, mean intensity at length 0, for species a, and the difference in the intercept value from species a to b. It provides a slope, fitting mean intensity with increasing length for species a, and an interaction parameter that describes any difference in slope between species a and b. P-values are provided for each parameter.

Software used for computing statistical analysis and creating graphs include R (version 3.0.1) and Microsoft Excel (2011).

Results

Temporal dynamics of Diphyllbothrium infections in Arctic charr

Prevalence

The temporal analysis of prevalence revealed a decrease for both parasite species after the fish reduction experiment (fig. 3). The prevalence was generally higher for *D. ditremum* than for *D. dendriticum*. There were fluctuations in prevalence between years for both parasite species, but the prevalence decreased gradually for *D. ditremum* from more than 90% in the 1980s, to less than 60% in the late 2000s. The decrease in prevalence was more abrupt for *D. dendriticum*. By 1987, the prevalence of *D. dendriticum* had been halved from around 80% before the manipulation, to less than 40%. Thereafter the prevalence fluctuated below 50% with the exception of 1993. The decreasing trend prevailed throughout the whole study period, with prevalence below 20% in six of the 11 years from 2001 and onwards. The linear regression showed that the decline in prevalence was significant for both *Diphyllbothrium* species ($p < 0,01$), but there was no significant difference between the declining prevalence slopes for the two species ($p > 0,05$).

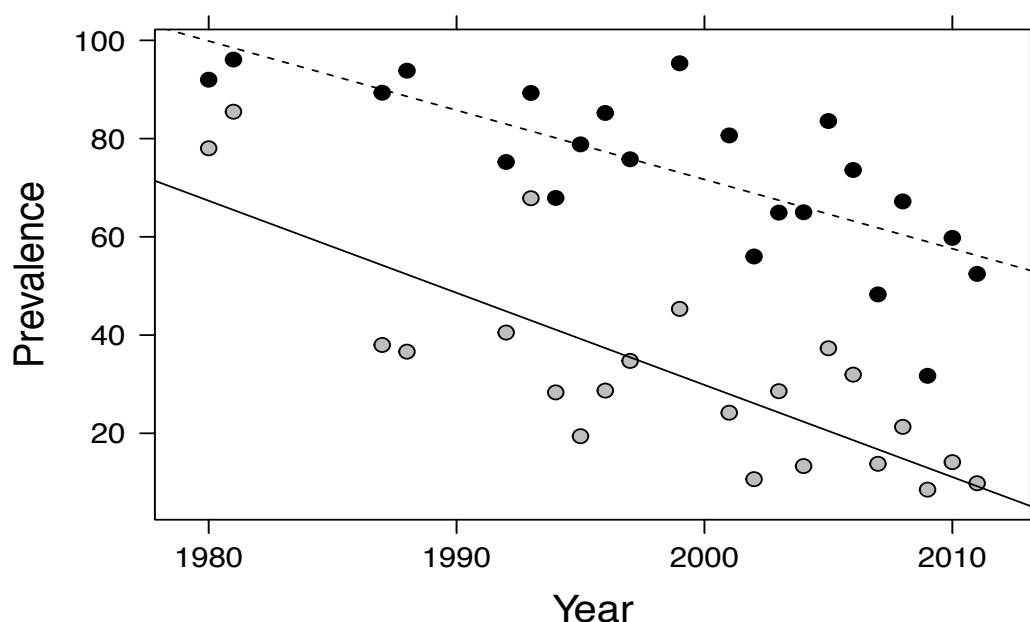


Fig. 3. Prevalence with linear regression lines for *D. ditremum* (black dots, dashed line) and *D. dendriticum* (Grey dots, solid line) in Arctic charr, for years sampled between 1980 and 2011. For n see tab. 1 and for exact values see appendix tab. 1 and 2.

Frequency distributions

Both for *D. ditremum* and *D. dendriticum*, the frequency of heavily infected individuals within the Arctic charr population decreased immensely from 1980-1981 to 2009-2011 (fig. 4). Prior to the implementation of the fish depletion experiment, most individuals of the Arctic charr population were infected by more than 10 plerocercoids of *D. ditremum*. The proportion of highly infected fish showed some reduction towards the mid 1990s, but in 1999 the frequency of intensities were similar to conditions prior to the fish-depletion. The proportion of Arctic charr with low infections of *D. ditremum* decreased in the 2000s, culminating with low frequencies of highly infected fish in 2009-2011. The infections of *D. dendriticum* were similar to *D. ditremum* prior to the culling of fish, but from 1987-1988 and onwards most of the Arctic charr harboured 0 or few parasites and very few fish had high infections.

Temporal dynamics of mean abundance and mean intensity

For both *Diphyllbothrium* species, the mean intensity increased from 1980 towards a peak in 1993 (fig. 5). Thereafter, the mean intensity strongly declined and fluctuated at low levels with peaks every five to seven years. A highly similar pattern was observed for the mean abundance, but for *D. dendriticum* there was no initial increase in mean abundance until the peak in 1993. The mean intensity and abundance are closely correlated, and were between 2,5 and 3 times higher for *D. ditremum* than for *D. dendriticum* prior to the fish depletion (see appendix tab. 1 and 2). The infections of *D. ditremum* remained higher than *D. dendriticum* throughout the study period, but the ratio of this difference varied between years and was in general higher for mean abundance than mean intensity. The standard errors and variance to mean ratios showed a general increase with higher values of mean intensity and mean abundance, and were particularly high in the years 1987 - 1993 (appendix tab. 1 and 2). The mean abundance was calculated for Arctic charr in a fixed size-group between 15 and 25 cm for all sampling years (fig. 6). Here, the mean abundance of *D. ditremum* increased from 1980-81 to 1987-88, thereafter decreasing with two smaller peaks of infection in 1999 and 2004. The infections of *D. dendriticum* in the same length group of charr decreased rapidly after 1981 and persisted at low infection levels until the end of the study.

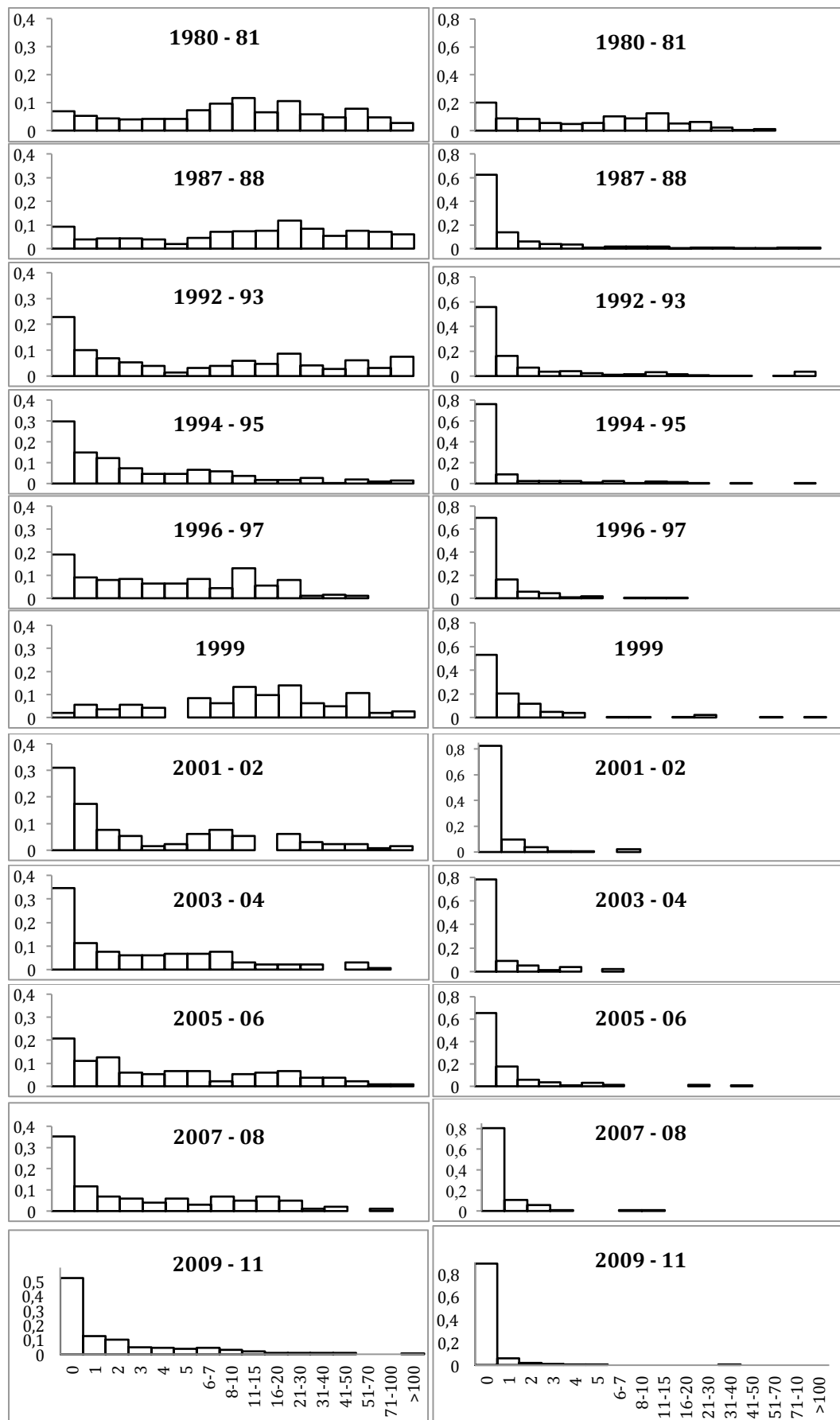


Fig. 4. Frequency distributions of *D. ditremum* (left) and *D. dendriticum* (right) infections in *A. charr*. Y-axis shows frequency of fish, note the differences in scale. The x-axis shows no. of plerocercoids.

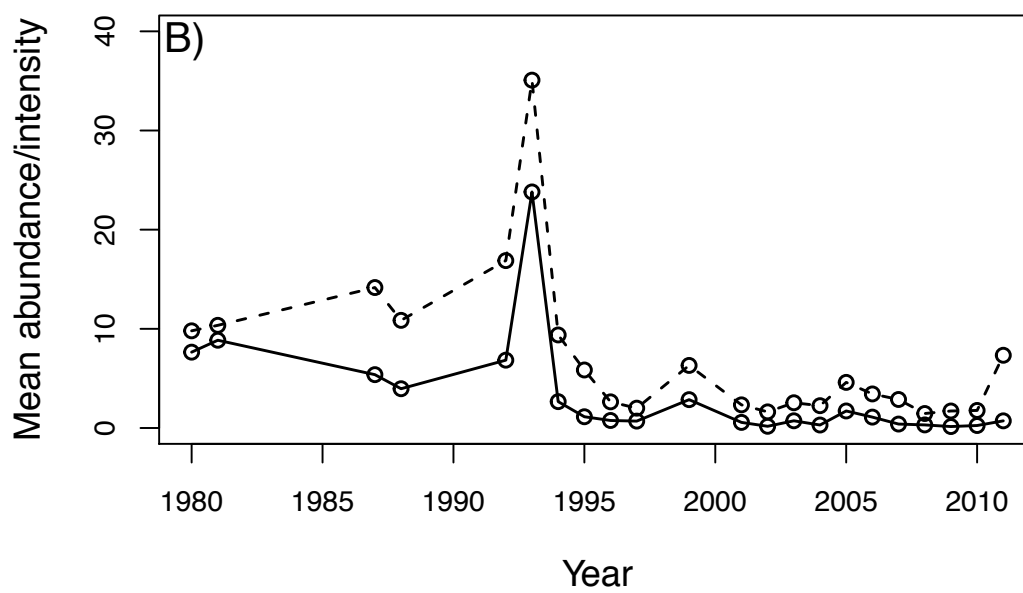
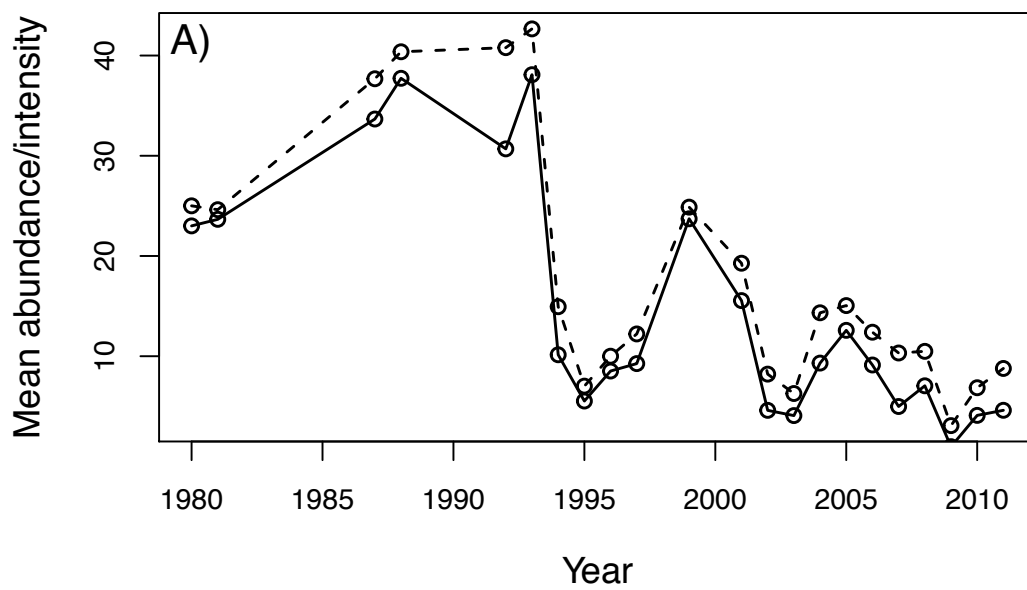


Fig. 5. Mean intensity (dashed line) and mean abundance (solid line) of *D. ditremum* (A) and *D. dendriticum* (B) in Arctic charr sampled between 1980 and 2011. For n see tab. 1. For exact values and standard errors see appendix tab. 1 and 2.

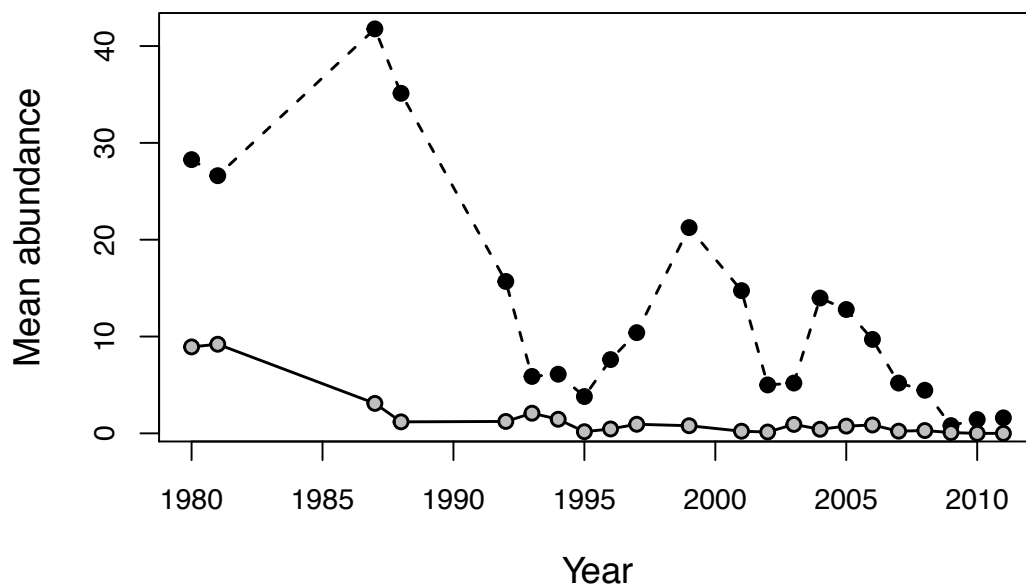


Fig. 6. Mean abundance of *D. ditremum* (dashed line) and *D. dendriticum* (solid line) in 15 - 25 cm long Arctic charr sampled between 1980 and 2011.

Relative intensity

The relative intensity showed a different temporal pattern than mean intensity (fig. 7). The linear regression revealed a significant decrease in mean relative intensity for both *Diphyllobothrium* species following the fish removal experiment ($p \ll 0.01$) (appendix fig. 1). The *D. ditremum* infection showed a marked decrease from > 36 plerocercoids/100 g fish up to 1988 to 14.7 in 1992 and further down to between 2-4 from 2008 and later, thus fluctuating in a similar pattern as described for mean abundance and mean intensity (fig.7). The relative intensity of *D. ditremum* was significantly higher than *D. dendriticum* ($p < 0.05$). The infection of *D. dendriticum* declined rapidly from 19.6 plerocercoids/100g in 1980 to 5.7 in 1988, thereafter fluctuating at a low level in a similar pattern as seen for *D. ditremum*.

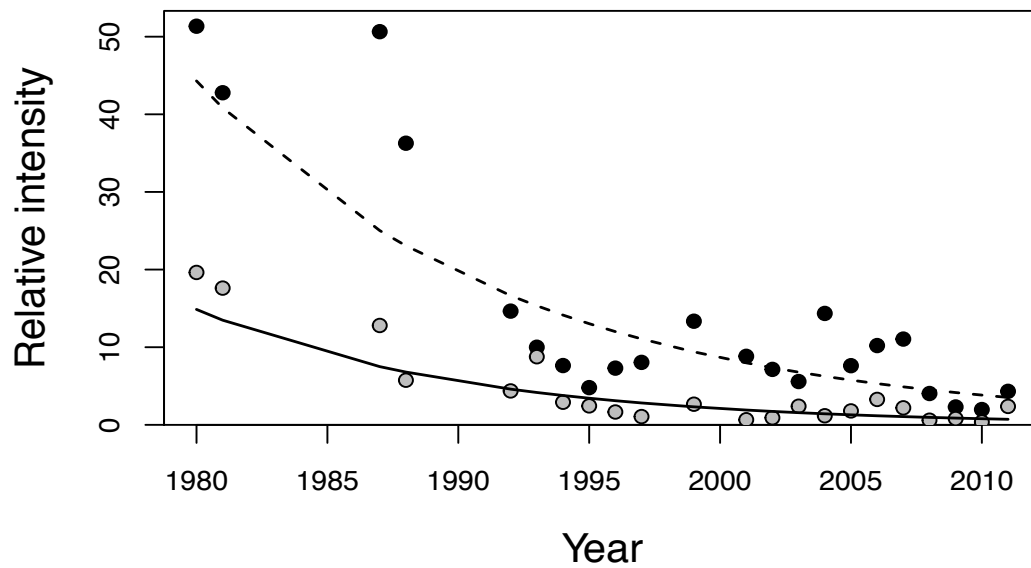


Fig. 7. Relative intensity (no. plerocercoids / 100 gram fish) of *D. ditremum* (black circles) and *D. dendriticum* (grey circles) in Arctic charr in all sampling years. Lines are fitted based on log y-values.

Infections of Diphylobothrium in Arctic charr versus brown trout

The prevalence of *D. ditremum* was significantly higher in Arctic charr than in brown trout (chi-square test, $p \ll 0,01$), being 61.5 *versus* 39.3 % for the two fish species, respectively (tab. 2). There was no significant difference in the intensities of *D. ditremum* between charr and trout (two-tailed permutation test, $p > 0.05$). For *D. dendriticum* the prevalence was highest in brown trout (chi-square test, $p \ll 0,01$) with 31.2 %, while 19.3 % of the Arctic charr were infected. The mean intensity of *D. dendriticum* was much higher in brown trout (25.0) than Arctic charr (3.0), and the intensities differed significantly between the two fish species (two-tailed permutation test, $p \ll 0.01$).

Table 2. Prevalence, mean abundance and mean intensity of *D. ditremum* and *D. dendriticum* infecting Arctic charr (n = 767, mean age = 4.4) and brown trout (n = 369, mean age = 3.9) sampled between 2001 and 2011. Standard errors in parentheses.

	Arctic charr	Brown trout	Arctic charr	Brown trout
	<i>D. ditremum</i>	<i>D. ditremum</i>	<i>D. dendriticum</i>	<i>D. dendriticum</i>
Prevalence	61,5	39,3	19,3	31,2
Mean abundance	6,7 (0,51)	5,3 (1,13)	0,6 (0,09)	7,8 (2,02)
Mean intensity	10,9 (0,78)	13,4 (2,75)	3,0 (0,43)	25,0 (6,17)

Intensity of infection through the ontogeny of the hosts

The fitted negative binomial GLM curves in figure 8 show that Arctic charr became slightly more infected with *D. ditremum* than brown trout with increasing fish length. However, there was no significant difference between the intercept (length = 0), or the interaction parameter (= rate of increase) for the two fish species ($p > 0,05$). For *D. dendriticum*, the infections in brown trout started to increase exponentially around 30 cm fish length, while the infections in Arctic charr remained low. The negative binomial GLM reveals that Arctic charr had significantly higher infections of *D. dendriticum* than brown trout at the intercept ($p < 0,05$), but the rate of increase was more than twice as large in brown trout than in charr ($p \ll 0,01$), which resulted in the observed pattern (fig. 8).

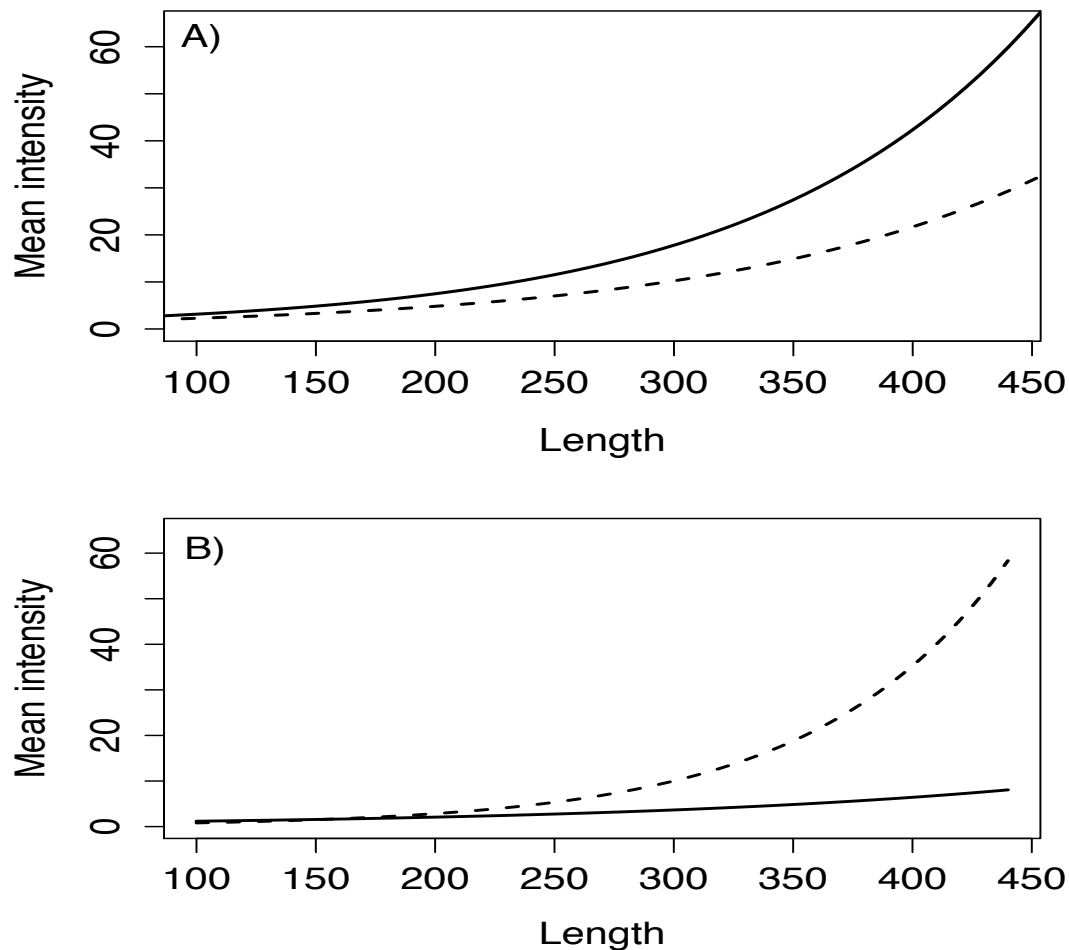


Fig. 8. Fitted negative binomial GLM for intensities of *D. ditremum* (A) and *D. dendriticum* (B) infecting Arctic charr (solid lines) and brown trout (dashed lines) sampled in the period 2001 – 2011. Uninfected fish are not included. The x-axis shows the length of the fish in mm.

Discussion

The long term monitoring of the two *Diphyllbothrium* component populations infecting Arctic charr revealed a profound decrease in prevalence, mean abundance and mean intensity over the three decades period from the years prior to the fish depletion until the last years of this study. The two *Diphyllbothrium* species displayed different temporal trends in infections, with *D. ditremum* increasing after the initiation of the fish removal before declining in the 1990s, while infections of *D. dendriticum* decreased more rapidly. Infections of both parasite species fluctuated quite regularly between years. The abundance of *D. ditremum* was higher in Arctic charr than in brown trout, whilst brown trout exhibited higher infections of *D. dendriticum* obtained at increasing fish lengths. The revealed infection dynamics of the two parasite species will be discussed in light of the large ecological changes that took place in the Takvatn ecosystem following the mass removal of Arctic charr.

As hypothesized, the abundances of both *Diphyllbothrium* species decreased significantly in the Arctic charr population over the three decades study period. Parasite infections are generally shown to correlate positively with host density both from theoretical (Dobson and May 1987, Dobson 1990) and empirical work (Morand and Poulin 1998, Arneberg et al. 1998, Kennedy et al. 2001). Heavy stock reduction/fishing is therefore expected to reduce parasitism (Lafferty et al. 2008b). However, for parasites with life cycles involving multiple host species, it is unclear which host's abundance is most important for parasite infection levels (Hansen and Poulin 2006), and the association between host densities and parasite infections is less clear (Arneberg 2001, Heins and Ecke 2012). The observed decrease in infection levels of *D. ditremum* and *D. dendriticum* could be caused by the reduced density of Arctic charr in the system (Klemetsen et al. 2002, Persson et al. 2007), as correlation between host density and parasite mean abundance in second intermediate hosts have been reported elsewhere (Hansen and Poulin 2006). Similarly, reducing the density of a European whitefish (*Coregonus lavaretus*) population led to decreased infections of the copepod-transmitted cestode *Trianeophorus crassus* which has whitefish as the second intermediate host (Amundsen et al. 2002). The decrease in infections of *D. dendriticum*, observed in the present study, correspond with the reduced density of Arctic charr. For *D. ditremum*, however, reduced infections occurred some years after

the fish removal programme was terminated, suggesting that other factors than fish density alone play a role.

The culling of fish in Takvatn induced changes in the prey populations of Arctic charr as well as in the Arctic charr population itself (Amundsen 1989, 1994, Dahl-Hansen 1995, Klemetsen et al. 2002, Persson et al. 2007). It is probable that these factors, rather than the isolated effect of a reduced density of intermediate fish hosts, are key to understand the observed temporal patterns in the *Diphyllbothrium* infections. Predator-prey relationships such as habitat choice and foraging behaviour may be important factors structuring the parasite component communities in fish (Esch 1971, Knudsen et al. 2004, 2008). The mass removal of Arctic charr increased the abundances of attractive benthic prey, notably the amphipod *Gammarus lacustris* and the snail *Radix peregra* (Amundsen et al. 1993). Likely as a result of this, there was a habitat-shift in small zooplanktivore Arctic charr from the profundal and pelagic zone to the littoral (Klemetsen et al. 1992, 2002, 2003). Simultaneously, the relative abundance and importance of cladocerans in the zooplankton community increased (Dahl-Hansen 1995; P.-A. Amundsen et al., unpublished data). Hence, the combined effects of the migration to the littoral habitat, increased abundances of littoral prey, a relatively higher proportion and abundance of cladocerans in the zooplankton community, and the subsequent change in the diet of Arctic charr away from copepods, are likely all important factors contributing to the observed decrease in the *D. ditremum* and *D. dendriticum* infections.

With respect to the temporal variations in the *Diphyllbothrium* infections in Arctic charr, the prevalence, mean abundance and mean intensity of *D. ditremum* were higher than for *D. dendriticum* in all sampling years. This is in accordance with findings from other sub-arctic lakes (Halvorsen 1970, Henricson 1977, Knudsen et al. 1997). A tolerance for lower temperatures for the developing stages of *D. ditremum* has been suggested as a factor explaining the higher success of *D. ditremum* compared to *D. dendriticum* in the sub-arctic (Halvorsen 1970). Differences in the biology of the avian final hosts has also been proposed as a mechanism behind this, as mergansers and divers are more specialized fish predators than omnivorous gulls (Hickey and Harris 1947, Henricson 1977).

The mean intensities and abundances were stable or increasing for both *Diphyllbothrium* species during and shortly after the culling. The peak observed in 1993 is most likely due to old and large-sized fish dominating the sample (see tab. 1), and overall, the prevalence, frequency distributions, relative intensity and mean abundance of 15 – 25 cm long fish suggest that there was a more rapid decrease in infections of *D. dendriticum* compared to *D. ditremum*. This rapid decline in infections could be caused by altered transmission rates to the final host population of gulls. In the stunted condition, infections of *Diphyllbothrium* spp. suggested parasite induced mortality in heavily infected Arctic charr, which acted as a negative feedback mechanism on the parasite population (Kristoffersen 1993). Such parasite-induced host mortality has previously been documented for *D. dendriticum* (Henricson 1977, Rahkonen et al. 1996), and Hickey and Harris (1947) suggested that fish mortality may be essential for the parasite in order to reach its final hosts that feed mostly on dead or dying fish. Consequently, an initial decline in *D. dendriticum* could have been reinforced through infections no longer reaching lethal levels in Arctic charr. Humans leaving fish entrails accessible to gulls may also be important in canalizing the transmission of *D. dendriticum* (Halvorsen 1970). Sensible handling of fish and their remains were emphasized locally in the culling period (Hope 1992), and this may have contributed to reducing the transmission to the final host.

Whereas the infections of *D. dendriticum* decreased shortly after the culling of fish began, the infection of *D. ditremum* in contrast showed an apparent increase at least until 1988. This unexpected response could be caused by Arctic charr increasing their consumption rates, which was observed when the population density was lowered (Amundsen 1989, Amundsen et al. 2007). This could have led to a higher net intake of copepods infected with *D. ditremum*. However, despite higher consumption rates, Amundsen (1989) found that Arctic charr consumed less copepods in the summer of 1986 compared to 1980. Kristoffersen (1993) proposed that Arctic charr were able to sustain higher infections of *D. ditremum* in the absence of *D. dendriticum*, which could explain the apparent increase in *D. ditremum* infections after the culling of fish.

From the 1990s and onwards, the two *Diphyllbothrium* species showed distinct inter-annual fluctuations in mean abundance, mean intensity and relative intensity as well as in the mean abundance within the 15 – 25 cm size-group of Arctic charr. Parasite

and host populations can exhibit parallel oscillations in systems where the parasite regulates the host population in a density-dependent manner, similar to predator and prey oscillations (Anderson and May 1978, Tompkins et al. 2002). The density of Arctic charr fluctuated between years after the fish removal experiment (Klemetsen et al. 2002, Persson et al. 2007, see also fig. 2), but the oscillations did not match the peaks of *Diphyllbothrium* spp. infection observed here. The low levels of infection after the culling do not indicate any parasite induced regulation of the Arctic charr population (Kristoffersen 1993), and shifting densities of Arctic charr in Takvatn are more likely linked to predation from brown trout (Persson et al. 2007). An oscillating pattern has been described for red foxes infected with the cestode *Echinococcus multilocularis*, where the infection cycles corresponded with the fluctuating abundance of, and hence predation upon, voles (*Clethrionomys rufocanus*), the intermediate host of *E. multilocularis* (Saitoh and Takahashi 1998). In my study, the peaks of infection in Arctic charr seem coincide with high population density of three-spined sticklebacks, which show cyclic oscillations with peaks every 6-7 years (Klemetsen et al. 2002, see also appendix fig. 2).

There are several possible explanations for how the fluctuations in stickleback density can affect infections of *Diphyllbothrium* in Arctic charr directly or indirectly. Firstly, Arctic charr can become directly infected with both *D. ditremum* and *D. dendriticum* through consumption of three-spined sticklebacks (Bérubé and Curtis 1986). The stickleback population of Takvatn have been shown to harbour many plerocercoids, especially of *D. ditremum* (Hope 1992, Jakobsen 2011). Sticklebacks have frequently been found in stomach samples of Arctic charr in Takvatn (Amundsen 1994) and piscivorous individuals have elevated infections of both *Diphyllbothrium* species (Knudsen et al. 1996). In years with high densities of three-spined stickleback high transmission rates of parasites to Arctic charr are therefore expected. Secondly, in years with high stickleback densities in Takvatn the relative abundance of copepods in the zooplankton community increases (Dahl-Hansen 1995). Three-spined sticklebacks are efficient zooplankton predators that can exert top-down control on the zooplankton community structure (Jakobsen et al. 2003). The typical reduction in large-bodied cladocerans (Jakobsen et al. 2003) may enhance the importance of copepods in the diet of zooplanktivorous Arctic charr, thereby indirectly increasing infection rates of the two *Diphyllbothrium* species. Empirical support for this is

found during the years with both low *Diphyllbothrium* infections and stickleback densities in the mid 1990s, when the importance of the cladoceran *Daphnia galeata* suddenly increased in the diet of Arctic charr (Klemetsen et al. 2002). Thirdly, high densities of three-spined sticklebacks may facilitate the life cycle of the two *Diphyllbothrium* species, as the sticklebacks are probably more important than salmonids in transmitting plerocercoids to the bird final host (Halvorsen 1970). The avian hosts for *D. ditremum* and *D. dendriticum* are predators of sticklebacks (Reimchen 1994), and the presence of sticklebacks has e.g. been shown to be a good predictor of the distribution of red-breasted mergansers (Råd 1980). Consequently, high densities of the stickleback population can lead to increased stickleback predation by avian hosts, especially red-breasted mergansers, causing higher infections in the birds and more cestode eggs, particularly of *D. ditremum*, being released into the lake. In this way, high densities of sticklebacks could lead to increased prevalence of *Diphyllbothrium* spp. in copepods, thereby indirectly enhancing the probability of transmission to zooplanktivorous Arctic charr. Finally, the three-spined stickleback population in Takvatn is infected with the diphyllbothriidean cestode *Shistocephalus solidus* (Hope 1992, Jakobsen 2011), which often co-occurs with *Diphyllbothrium* spp. in infected sticklebacks (Hope 1992). Individuals infected with *S. solidus* have reduced anti-predator behaviour (Giles 1983, Barber et al. 2000). As higher host densities is expected to increase parasite transmission (Morand and Poulin 1998, Arneberg et al. 1998), years with high stickleback densities could lead to higher infections of *S. solidus*. Consequently, in these years sticklebacks may be more easily predated upon by both birds and Arctic charr, thereby facilitating the transmission of the two *Diphyllbothrium* species.

The cyclic pattern observed in the *Diphyllbothrium* infections is intriguing, and could likely be caused by oscillations in the density of three-spined sticklebacks. The most obvious factors for this are that the presence of sticklebacks maintains a larger population of avian final hosts, and that the sticklebacks can increase the transmission of *Diphyllbothrium* through piscivory, especially when they are infected with *S. solidus*. Mass die-offs have been observed in 3-spined stickleback populations heavily infected with *S. solidus* (Threlfall 1968). Parasites that induce mortality in hosts may cause a stable cyclic pattern in host and parasite population size (Anderson and May 1978), and *S. solidus* may therefore be a driver in the fluctuating nature of the

stickleback population in Takvatn. This notion is worth further investigation as no unequivocal evidence of fish host and parasite populations undergoing linked stable cycles exist (Kennedy 2009).

Finally, it was hypothesized that the infections of *Diphyllbothrium* would differ between brown trout and Arctic charr, reflecting their trophic niches in sympatry. Arctic charr had a higher prevalence of infection of *D. ditremum* than brown trout, but the intensities did not differ significantly between the two fish species. Brown trout had a higher prevalence of *D. dendriticum*, and also a higher mean abundance and intensities, especially with increasing fish lengths. Phylogenetic specificity and parasite-host compatibility are two factors that can create dissimilarities in helminth infections between fish species (Lagrué et al. 2011) due to e.g. differences in the immune responses of the hosts (Secombes and Chappell 1996). The tissue immune response exhibited when infected with *Diphyllbothrium* plerocercoids seems to be poorly developed in salmonids (Bylund 1972, Sharp et al. 1992). However, it cannot be ruled out that the success of *D. ditremum* and *D. dendriticum* in establishing infections differs between Arctic charr and brown trout, thus creating the infection pattern observed here.

Ecological differences in feeding or habitat utilization may be more important than immunological factors for observed discrepancies in the parasite acquisitions of fish hosts (Knudsen et al. 1996, 2004, 2008). When co-occurring, brown trout is found to restrict the habitat use and foraging behaviour of Arctic charr during summer and autumn by dominating in the littoral zone (Nilsson 1963, Langeland et al. 1991, Eloranta et al. 2013). They also segregate in diet with brown trout feeding on zoobenthos and pleuston while Arctic charr forage on zooplankton (Langeland et al. 1991, Jansen et al. 2002, Eloranta et al. 2013). The segregation in diet is maintained even when both species are found sympatrically within the littoral zone (Eloranta et al. 2013). The infections of both *Diphyllbothrium* species in Arctic charr and brown trout in the current study can to some extent reflect the different niches of these two fish species in sympatry. The higher prevalence observed for *D. ditremum* indicates that Arctic charr are feeding more on zooplankton than brown trout, and the elevated intensities in large charr could support the notion that even large Arctic charr to a greater extent are zooplankton feeders when coexisting with brown trout (Nilsson

1963). Interestingly, the infections of *D. dendriticum* was higher in brown trout, with a mean intensity 8-folds greater than in Arctic charr. *Diphyllobothrium dendriticum* seem to be more successful than *D. ditremum* at re-establishing in piscivorous fish (Halvorsen and Wissler 1973), and the parasite may tend to aggregate in piscivorous individuals (Halvorsen 1970). Knudsen et al. (2008) found *D. dendriticum* to be a suitable indicator for piscivorous feeding, and the high infections of large brown trout observed here suggest that these infections are acquired through piscivory. The prevalence and mean intensity of *D. ditremum* in brown trout was higher than expected, and also high in comparison with findings from another lake in northern Norway lake with identical fish fauna to Takvatn (Knudsen et al. 2008). If these infections were acquired through predation upon infected copepods it would suggest that 40 per cent of the brown trout population have regularly been feeding copepods at a similar or higher rate than Arctic charr. This would contradict existing theory and findings both from Takvatn (Eloranta et al. 2013) and other, similar lakes (Langeland et al. 1991, Knudsen et al. 2008, Amundsen and Knudsen 2009). Similarly as for *D. Dendriticum*, most of these infections are probably obtained through piscivory, which has been described for piscivorous individuals harbouring *D. ditremum* elsewhere (Hammar 2000, Gallagher and Dick 2010). Around a length of 150 mm brown trout can start predated on small fishes, and the extent of piscivory and the prey-size range usually increase with with increasing length (L'Abée-Lund et al. 1992, Klemetsen et al. 2003). This scenario is supported by the exponential increase in *D. dendriticum* infections as the brown trout in Takvatn grow larger. However, the higher infection level of *D. dendriticum* also suggests that the susceptibility of brown trout for re-infection from fish prey is much higher for this parasite species than for *D. ditremum*, as also have been indicated from previous studies (Halvorsen & Wissler 1973). The observed infection patterns seem to correlate to dietary segregation between the two fish species, where large-sized brown trout is feeding heavily on three-spined sticklebacks or Arctic charr whereas piscivory is much less pronounced in Arctic charr. This is in accordance with the diet utilization derived from isotopic analyses of muscle tissue from an earlier study in Takvatn (Eloranta et al. 2013).

The large changes in the fish populations and their prey communities induced by the fish removal experiment in Takvatn have been well documented (Amundsen et al. 1993, Dahl-Hansen 1995, Klemetsen et al. 2002, Persson et al. 2007). Combining

such data on fish populations and their habitat use with parasitological observations is important for understanding how ecological factors influence the transmission of parasites to northern fishes (Curtis 1995). Here, I have shown how the infections of two *Diphyllbothrium* species in Arctic charr responded to a mass removal of the host. The changes in habitat and diet, important factors in increasing the growth of Arctic charr (Klemetsen et al. 2002), seem influential for the population decrease of both *Diphyllbothrium* species as well. The importance of a diet switch from zooplankton to benthic invertebrates, in reducing copepod-transmitted cestodes in fish populations has also been emphasized through culling experiments performed on stunted European whitefish and brook charr (*Salvelinus fontinalis*) populations (Curtis 1995, Amundsen et al. 2002). For management purposes, reducing the density of a stunted fish population can reduce copepod-transmitted parasite burdens as well as increasing the growth of fish, thereby improving the fish quality for human harvest.

The increased growth rate of Arctic charr may have altered the transmission rates of both *Diphyllbothrium* species to their avian final hosts by fish rapidly growing out of the predation window of birds, that typically feed on small-sized fish (Nilsson and Nilsson 1976, Doornbos 1984). Moreover, the larger fish that harbour most parasites are likely dead-ends in the life cycle of the parasites (Halvorsen 1970). Combined, this could have a large impact on the abundance of the two parasite species. However, both *Diphyllbothrium* species have been able to sustain their component populations despite the rapid somatic growth of Arctic charr and brown trout. Parasite populations are more likely to persevere when there are multiple competent hosts present (Curtis 1995, Hatcher et al. 2012). My results supports the notion of Amundsen et al. (2013), who suggested that the introduction of three-spined stickleback, and its host-manipulating cestode *S. solidus*, likely has increased the transmission rate and abundance of trophically transmitted parasites to piscivorous birds and fish in Takvatn. This implies that the fish culling would have had an even more severe effect on the two *Diphyllbothrium* populations in the absence of three-spined stickleback. The analysis of *Diphyllbothrium* infections in sympatric Arctic charr and brown trout could indicate diet segregation between the two fish species, where Arctic charr are feeding more on zooplankton and brown trout more on fish. Reduced piscivory by Arctic charr through interspecific competition from the increasing brown trout

population could therefore also be a factor in the vast reduction of *D. dendriticum* infection observed in the temporal analysis of charr.

The study of long-term data is essential in advancing our knowledge of the parasite-host relationship (Anderson 1991, Kennedy 2009). Temporal variations in prevalence and density of parasite populations can be the result of environmental perturbation or variability in the behaviour of potential intermediate or final hosts (Esch et al. 1986). Klemetsen et al. (2002) had unanswered questions regarding the stability in Takvatn 10 years after the end of the fish removal experiment. The present study shows that the infections of *Diphyllbothrium* had not stabilized by 2011, and the effects of the culling seem to still be echoing in the system. Kennedy (2009) proposed that helminth parasite communities in freshwater fish are unstable stochastic assemblages rather than stable entities. The parasite-host relationship described here may be in a perpetual dynamic where the importance of different interactions varies between years. It is evident that parasite-host interactions are pivotal in furthering our knowledge of ecosystem processes (Marcogliese and Cone 1997, Hudson et al. 2006, Lafferty et al. 2008a), and this study has highlighted how these interactions are sensitive to and indicative of ecological processes in a freshwater ecosystem.

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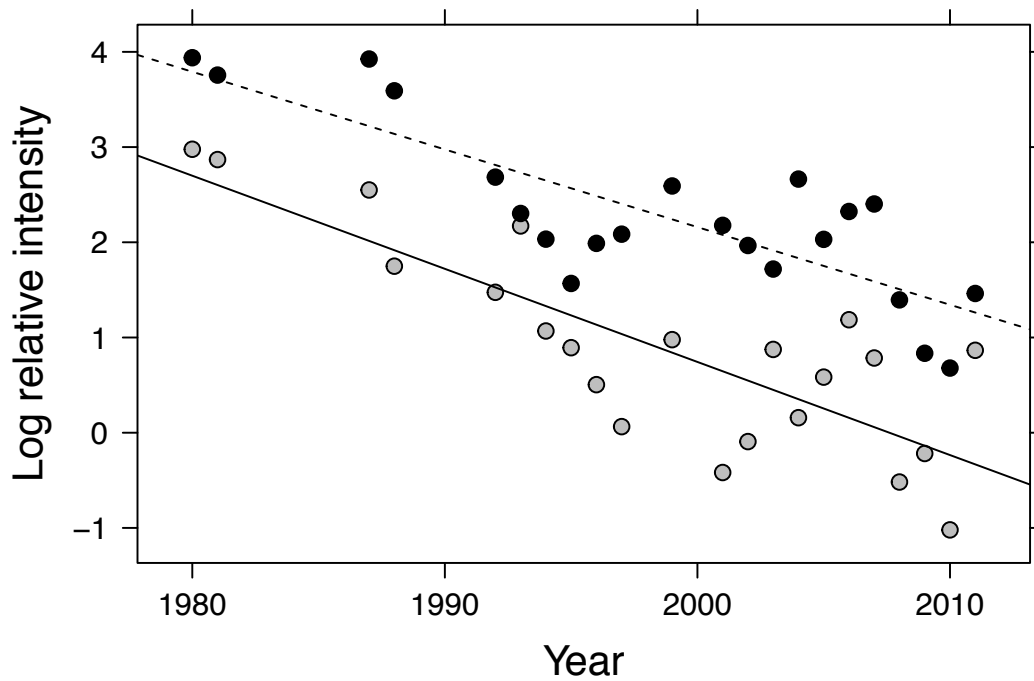
Appendix

Appendix table 1. Infections of *Dipyllobothrium ditremum* in Arctic charr in sampled years. Standard error in parentheses. Variance to mean ratios include infected and uninfected fish (i.e. is based on abundance data).

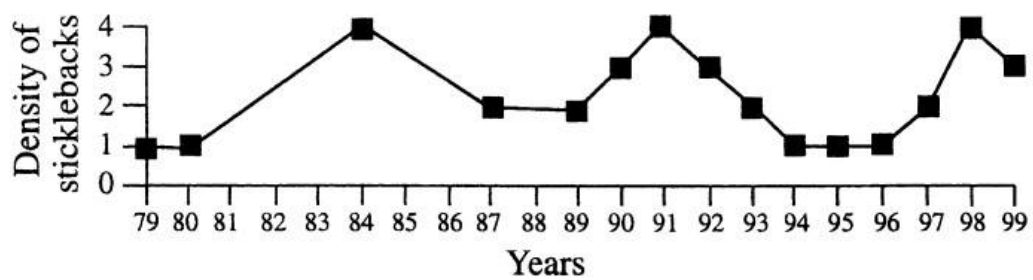
Year	Prevalence	Mean abundance (± SE)	Mean intensity (± SE)	Relative intensity	Var / mean (abundance)
1980	92.0	23.0 (1.3)	25.0 (1.3)	51.4	33.6
1981	96.1	23.7 (2.2)	24.6 (2.2)	42.8	34.7
1987	89.3	33.7 (2.8)	37.7 (3.1)	50.6	117.5
1988	93.8	37.9 (3.8)	40.4 (4.0)	36.3	93.8
1992	75.2	30.7 (4.1)	40.8 (5.2)	14.7	166.3
1993	89.3	38.1 (11.0)	42.7 (12.2)	10.0	175.5
1994	67.9	10.2 (1.6)	14.9 (2.3)	7.6	61.5
1995	78.8	5.5 (1.0)	7.0 (1.3)	4.8	31.5
1996	85.2	8.5 (1.2)	10.0 (1.3)	7.3	17.7
1997	75.8	9.3 (1.3)	12.2 (1.5)	8.1	16.6
1999	95.3	23.7 (2.3)	24.9 (2.3)	13.4	32.0
2001	80.7	15.6 (3.2)	19.3 (3.8)	8.8	39.7
2002	56.0	4.6 (1.4)	8.2 (2.3)	7.1	30.3
2003	64.9	4.1 (0.7)	6.3 (0.9)	5.6	8.3
2004	65.0	9.3 (2.3)	14.3 (3.3)	14.4	34.4
2005	83.6	12.6 (2.1)	15.1 (2.4)	7.6	23.1
2006	73.6	9.1 (2.0)	12.4 (2.6)	10.2	31.9
2007	48.3	5.0 (1.3)	10.3 (2.3)	7.7	19.4
2008	67.2	7.1 (1.6)	10.5 (2.2)	4.0	19.7
2009	31.7	1.0 (0.3)	3.1 (0.7)	2.3	6.0
2010	59.8	4.1 (0.9)	6.9 (1.4)	2.0	17.3
2011	52.5	4.6 (1.8)	8.8 (3.3)	4.3	42.9

Appendix table 2. Infections of *Diphyllbothrium dendriticum* in Arctic charr in sampled years. Standard error in parentheses. Variance to mean ratios include infected and uninfected fish (i.e. is based on abundance data).

Year	Prevalence	Mean abundance (± SE)	Mean intensity (± SE)	Relative intensity	Var / mean (abundance)
1980	78.0	7.7 (0.5)	9.8 (0.5)	19.6	12.9
1981	85.5	8.9 (0.7)	10.4 (0.8)	17.6	9.9
1987	38.0	5.4 (1.7)	14.2 (4.5)	12.8	284.6
1988	36.6	4.0 (1.1)	10.9 (2.8)	5.8	72.5
1992	40.5	6.8 (1.9)	16.9 (4.5)	4.4	159.9
1993	67.9	23.8 (0.1)	35.1(14.6)	8.8	234.9
1994	28.3	2.7 (0.8)	9.4 (2.6)	2.9	53.4
1995	19.4	1.1 (0.5)	5.9 (2.4)	2.4	36.2
1996	28.7	0.8 (0.2)	2.6 (0.6)	1.7	6.2
1997	34.7	0.7 (0.1)	2.0 (0.2)	1.1	2.1
1999	45.3	2.9 (1.1)	6.3 (2.4)	2.7	64.8
2001	24.2	0.6 (0.2)	2.3 (0.4)	0.7	3.0
2002	10.7	0.2 (0.1)	1.6 (0.6)	0.9	3.1
2003	28.6	0.7 (0.2)	2.6 (0.4)	2.4	2.9
2004	13.3	0.3 (0.1)	2.3 (0.7)	1.2	3.3
2005	37.3	1.7 (0.8)	4.6 (1.9)	1.8	22.6
2006	31.9	1.1 (0.4)	3.4 (1.0)	3.3	8.7
2007	13.8	0.4 (0.2)	2.9 (0.9)	2.2	4.6
2008	21.3	0.3 (0.1)	1.5 (0.2)	0.7	40.7
2009	8.5	0.2 (0.1)	1.7 (0.4)	0.8	2.0
2010	14.1	0.3 (0.1)	1.8 (0.3)	0.4	2.2
2011	9.8	0.7 (0.5)	7.3 (5.0)	0.8	23.6



Appendix fig. 1. Relative intensity, on a natural logarithmic scale, with linear regression lines for *D. ditremum* (black dots, dashed line) and *D. dendriticum* (Grey dots, solid line) infecting Arctic charr. For years sampled between 1980 and 2011.



Appendix fig. 2. Population density scores for littoral three-spined sticklebacks in Takvatn in the period 1979-1999. From Klemetsen et al. 2002.