Fish culling reduces tapeworm burden in Arctic charr by increasing parasite mortality rather than by reducing density-dependent transmission

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Abstract

1. Two common *Dibothriocephalus* (formerly *Diphyllobothrium*) tapeworm species were significantly reduced by experimental culling of their fish host Arctic charr (*Salvelinus alpinus*) in a subarctic lake.
2. Between 1984 and 1991, funnel traps were used to cull ~ 35 metric tons of Arctic charr, reducing charr density by ~ 80%. As charr densities decreased, tapeworm prevalence and then intensity also declined over the following three decades, with *D. dendriticus* (formerly *dendriticum*) responding faster than *D. ditremus* (formerly *ditremum*). The two main hypotheses for how culling a host can decrease parasitism are reductions in parasite transmission due to reduced host density and reductions in parasite survival through increases in host mortality rates.
3. We found little evidence that charr density was the main driver for reduced parasite transmission. Instead, decreased survivorship in charr, initially, through fishing-induced changes in charr age structure, and later through increased predation rates by brown trout, led to increased parasite mortality. Although brown trout, which increased significantly after fish culling, are also hosts, they are often too big for the final host birds to eat, thus becoming parasite sinks.
4. *Synthesis and applications*. Fish populations with heavy parasite burdens constitute a management problem. Our results show how fish culling reduce indirectly transmitted parasites through increased parasite mortality. Managing overcrowded fish populations by culling can produce two desirable outcomes: an increase in fish growth rates and reduced parasite burdens.

Keywords

Host culling, fish parasites, *Diphyllobothrium*, *Dibothriocephalus*, long-term study, whole-lake experiment, host-parasite interactions, fishing

Introduction

Fishing alters host density, age, and size structure, each of which might indirectly affect parasite transmission (Kapel & Fredensborg, 2015; Wood, Lafferty, & Micheli, 2010). As a result, fished stocks often have fewer parasites than unfished stocks (Amundsen & Kristoffersen, 1990; Dobson & May, 1987; Lafferty, 2008; Wood, Lafferty, & Micheli, 2010). For instance, fishing reduced the prevalence of bucephalid trematodes in scallops (Sanders & Lester, 1981), Black (1983) speculated that trout fishing extirpated a swimbladder nematode from the Great Lakes, and experimental fish culling reduced the prevalence of a whitefish *Coregonus lavaretus* (L.) tapeworm (Amundsen & Kristoffersen, 1990). On the other hand, fishing large individuals can lead to crowded, stunted, and heavily infected fish (Amundsen & Klemetsen, 1988). To investigate how fishing of the host population affects transmission and survivorship of two fish tapeworm species, we tracked how parasite prevalence and intensity changed along with Arctic charr *Salvelinus alpinus* (L.) density, age, and size structure before, during, and after fish culling.

As parasite transmission increases with host density (e.g. Arneberg, Skorping, Grenfell, & Read, 1998; Dallas, Krkošek, & Drake, 2018; Hechinger & Lafferty, 2005; Kennedy, Shears, & Shears, 2001), fishing could drive host populations below a critical host-density threshold, thereby reducing parasite establishment (Dobson & May, 1987). Although this is easy to demonstrate in simple host-parasite models, there are several reasons fishing might not impair transmission. To what degree fishing interrupts transmission depends on the scale of the fishery,

the scale of host recruitment and the scale of parasite recruitment (Kuris & Lafferty, 1992). In addition, generalist parasites that can use several different host species should be less sensitive to fishing than specialists (Lafferty, 2012; Wood & Lafferty, 2015). Furthermore, parasites occur in complex food webs, with several opportunities for indirect effects (Lafferty, 2004; Sonnenholzner, Lafferty, & Ladah, 2011) dependent on how fishing affects competitors, predators, and prey. Such effects are most likely for parasites that have complex life cycles with multiple hosts like tapeworms. For instance, culling second-intermediate and final hosts (whitefish and pike *Esox lucius*, respectively) reduced the prevalence of the tapeworm *Triaenophorus crassus*, but the prevalence of another tapeworm, *Dibothriocephalus ditremus*, formerly *Diphyllobothrium ditremum* (the revised genus name *Dibothriocephalus* (Waeschenbach, Brabec, Scholz, Littlewood & Kuchta, 2017) is used throughout the text), that uses piscivorous birds as a final host only decreased after whitefish switched their diet away from the first intermediate copepod host (Amundsen & Kristoffersen, 1990). For these reasons, fishing effects on parasites seem dependent on parasite life cycles, food-web structure, and fishing regulations (Wood & Lafferty, 2015; Wood et al., 2010; Wood, Sandin, Zgliczynski, Guerra, & Micheli, 2014). If and how fishing affects parasites depends on the details.

In addition to reducing transmission, fisheries could directly reduce parasite abundance in fished species by removing parasites. Specifically, mortality might increase for parasite species that accumulate with host age and size (e.g. Zelmer & Arai 1998; Cardon, Loot, Grenouillet, & Blanchet, 2011) if the fishery targets the largest and most heavily infected fish (Wood & Lafferty, 2015; Wood et al., 2010, 2014). However, when overcrowded fish populations have both stunted growth rates and high parasite burdens (Amundsen, Kristoffersen, Knudsen, & Klemetsen, 2002; Ylikarjula, Heino, & Dieckmann, 1999), it becomes less clear how fishing will affect fish size and associated parasitism. Potentially, culling could both increase fish

growth rates (by releasing individuals from competition) and decrease parasitism (e.g. by reducing fish age), and thereby make the fish more suitable for harvest (Amundsen et al., 2018).

Fish-borne parasitic zoonoses are a manageable threat to public health (Chai, Darwin Murrell, & Lymbery, 2005). Among the most common is Diphyllobothriasis, caused by tapeworms of the *Dibothriocephalus* genus. Estimated to infect ~ 20 million people worldwide, these several meters long tapeworms can infect people that eat undercooked fish (Chai, Darwin Murrell, & Lymbery, 2005; Curtis & Bylund, 1991; Dick, 2007; Scholz, Garcia, Kuchta, & Wicht, 2009). Furthermore, *Dibothriocephalus* larvae can slow fish growth and make infected fish unsightly (Blanar, Curtis, & Chan, 2005; Kuhn, Frainer, Knudsen, Kristoffersen, & Amundsen, 2016). In fact, high infection of *Dibothriocephalus* spp. and slow growth of the Arctic charr from subarctic Lake Takvatn in the early 1980s inspired a charr-culling experiment between 1984 and 1991. At this site, historical overfishing had shifted the system from a productive brown trout fishery to a crowded, stunted and heavily infected charr population (Amundsen & Klemetsen, 1988). To restore the fishery, the culling experiment was undertaken to reduce charr density and reset the system (Amundsen, Klemetsen, & Grotnes, 1993; Klemetsen et al., 2002). This fish culling led to larger charr size, a comeback of the brown trout population, and has been followed by continuous monitoring studies (e.g. Amundsen, Knudsen, & Klemetsen, 2007; Amundsen et al., 2018; Klemetsen et al., 2002; Persson et al., 2007).

Here we investigate how fish culling affected *Dibothriocephalus dendriticus* and *D. ditremus* infections in Arctic charr. We asked, (1) did culling reduce *Dibothriocephalus* spp. prevalence and intensity in Arctic charr? and (2) are long-term trends in *Dibothriocephalus spp.* infections governed by charr density, demography or brown trout density? Fishing could reduce *Dibothriocephalus* spp. in charr by reducing charr density and age (Klemetsen et al., 2002).

However, the tapeworm *D. ditremus* should be less sensitive to fishing because it uses unfished stickleback as an alternative host in Takvatn to a much larger extent than *D. dendriticus* (Folstad, Hope, Karter, & Skorping, 1994; Kuhn et al., 2015). Additionally, the increasing brown trout population (Persson et al., 2007) could reduce tapeworm transmission rates to birds because the most heavily infected piscivorous trout are too large for birds to catch, and might therefore act as parasite sinks (Henriksen et al., 2016).

Materials and methods

Study site

Takvatn (69°07´N, 19°05´E) is a 15 km^2 large and 80 m deep lake located in the Målselv River system in Troms county, northern Norway. It lies 214 m above sea level, and is typically ice-covered from November to early June. The lake is oligotrophic with Secchi depths ranging between 14 and 17 m, and phosphorous levels not exceeding 5 $\mu g\ L^{-1}$ (Eloranta, Knudsen, & Amundsen, 2013). The lake has three fish species; brown trout (*Salmo trutta*), Arctic charr, and three-spined sticklebacks (*Gasterosteus aculeatus*) (hereafter referred to as trout, charr and sticklebacks). The trout is the only native fish species in Takvatn, whereas charr was introduced in 1930 and sticklebacks in 1950 (from nearby lakes). By 1980, the fish community in Takvatn had a dense population of stunted charr (Amundsen & Klemetsen, 1988), whereas trout were rare (Amundsen et al., 1993). Between 1984 and 1991, intensive fishing with baited funnel traps removed ~720 000 (~35 metric tons) charr from the lake, reducing the density by ~ 80% (Amundsen et al., 1993, 2018; Klemetsen et al., 2002). This resulted in a new stable state with coexisting large charr and trout (Amundsen et al., 2018; Klemetsen et al., 2002; Persson et al., 2007).

Sampling

Charr individuals analysed in the present study were sampled in the years 1980, 1981, 1987, 1988 and every year between 1992 and 2016 except in 1993, 1998, 2000 and 2014, thereby covering the periods before, during and 25 years after the fish removal experiment. Fish were sampled in August each year using bottom (40 m × 1.5 m) and floating (40 m × 6 m) gillnets. In some years, additional months were sampled, but as the parasites live for several years in the fish (Halvorsen & Andersen, 1984), we did not observe significant monthly variation in *Dibothriocephalus* infections. Thus, we included the available additional samples to increase our sample size. Net series with bar mesh sizes from 10 to 52 mm knot to knot were used prior to 1989. From 1989 and onwards, we used multi-mesh nets with eight panels ranging from 10 to 45 mm knot to knot. The nets were left overnight for ~12 hours in the lake. Fish were collected from the littoral (< 15 m depth), profundal (25 – 40 m depth) and pelagic (offshore, > 30 m depth) zones of the lake (see Klemetsen et al., 2002 for further sampling details). Fish were weighed, measured in fork length, and sex and gonad maturation were recorded. Otoliths were used for age determination. Charr and trout densities were measured as CPUE (fish caught per $100m^2$ gillnet per night during the August sampling periods averaged over different habitats). Fish tissue containing *Dibothriocephalus* was placed in a digestive fluid, mimicking the stomach environment of the final bird host, containing 2 ml HCL, 5 g pepsin, 9 g NaCl in 1 L water to excyst the parasites (Knudsen & Klemetsen, 1994). The excysted parasites were conserved in 4% buffered formalin and later identified to species with a stereo microscope following Andersen & Gibson (1989).

Parasite life cycles

The two cestodes *Dibothriocephalus dendriticus* and *D. ditremus* have a circumpolar distribution (Andersen, Ching, & Vik, 1987). Both parasites are trophically transmitted in a three-host life cycle. The first-intermediate hosts are cyclopoid and calanoid copepods (Halvorsen, 1966; Marcogliese, 1995; Scholz et al., 2009). Their second-intermediate hosts are typically salmonid fish species, but they may also use sticklebacks (Halvorsen, 1970; Vik, 1964). The larval stage can survive several years in the fish, and older fish sometimes accumulate many larvae (Halvorsen & Andersen, 1984). Both parasite species can also be transmitted from fish to fish through piscivory (Curtis, 1984; Halvorsen & Wissler, 1973), though *D. dendriticus* has a higher probability of re-establishing in piscivorous fish (Halvorsen & Wissler, 1973). Gulls are the main hosts for *D. dendriticus* (Halvorsen, 1970; Vik, 1964), whereas diving birds like red-breasted mergansers (*Mergus serrator* L.) and divers (*Gavia* sp.) are the main hosts for *D. ditremus* (Vik, 1964). Our results, therefore, might apply only to parasites with complex life cycles.

Data analyses

Parasite prevalence, mean abundance and median intensity (Bush, Lafferty, Lotz, & Shostak, 1997) were calculated each year for each tapeworm species. Median intensity is used instead of mean intensity because in years with few infected fish, the median is less sensitive to outliers (Rózsa, Reiczigel, & Majoros, 2000). We interpolated missing years using the “Na.spline” function from the *Zoo* package (Zeileis & Grothendieck, 2005) in R (R Core Team, 2018). We compared correlations between variables in the splined dataset to correlations in the original data to check that interpolating had not changed the relationship between any of our variables. The splined dataset was used in the subsequent breakpoint analyses and GLS models (see below). We used breakpoint analysis to identify temporal changes to the system, using the function “segmented” from the *segmented* package (Muggeo, 2008) in R. This analysis fits

199 regression coefficients to a variable and estimates the time point when coefficients change, i.e.
200 there are two different linear trends on each side of the breakpoint. The slope and confidence
201 intervals (CI) for the two linear trends are provided, as well as the R-squared value for their
202 combined fit.
203
204 Infections in the charr population could change because of other ecological factors than altered
205 parasite abundance in the ecosystem, for instance through truncated age structure or diet shifts
206 in older charr. If so, the *Dibothriocephalus* spp. infection pressure on young charr, the
207 ontogenetic stage where charr feeds most on zooplankton (Amundsen, Knudsen, & Klemetsen,
208 2008), should remain constant. We used logistic regression to analyse if the relationship
209 between infection and charr age changed before, during, and over four 5-year periods after
210 culling. Infection was the binomial response variable and charr age the predictor. From these
211 models, we calculated the age at which there was a 50% probability of charr being infected with
212 *Dibothriocephalus* spp. Models for individual years showed a similar pattern as the overall
213 periods, and results from these are provided in the supplementary material (Tables S4, S5).
214
215 To track relative changes in the parasite component population ('ecological abundance' *sensu*
216 Wood et al., 2013) of the two *Dibothriocephalus* species in charr, we multiplied the mean
217 abundance of the respective parasite species per charr by charr density (CPUE) within each
218 year.
219
220 Finally, we tested associations between *Dibothriocephalus* spp. intensity and prevalence, and
221 predictor variables (charr age, length, density and trout density) with generalized least squares
222 (GLS) models fit using GLS from the R package *nlme* (Pinheiro et al., 2018). In all models, we
223 controlled for autocorrelation using either an autoregressive term, AR1, or moving average

term, MA1, following the "auto.arima" function from the R *forecast* package (Hyndman & Khandakar, 2008). Model fit was evaluated by checking ACF (autocorrelation function) and PACF (partial autocorrelation function) and the fit between standardized residuals vs fitted values. Non-significant predictors were removed and models were refitted and re-evaluated using AIC values to choose the most parsimonious model. Trout CPUE was transformed (log +1) to meet parametric assumptions. Given the possibility that temporal lags could affect the relationship between host and parasite dynamics, we also fitted models with a 1-year lag in charr and trout densities. However, the lagged models fitted poorly and are not presented here.

Changes in predator (trout) and charr density could affect parasite intensity and prevalence indirectly through changes in charr age and size structure. Therefore, we tested for both direct (fish density affects parasites directly) and indirect (fish density affects charr age and size which affects parasites) relationships using piecewise structural equation modelling (SEM). Piecewise SEM allows the simultaneous test of multiple relationships while controlling for potential correlations using a set of GLS models that describe all hypothesized direct and indirect relationships in the data. The results from our piecewise SEM did not differ from the individual GLS models described above (i.e. we did not detect indirect relationships between trout or charr density and charr age and size (all $p > 0.05$)). Thus, we only present the individual GLS results here.

Results

Did culling reduce *Dibothriocephalus* spp. infections in charr?

The prevalence and intensity of *D. dendriticus* decreased soon after the culling started (in 1984) and remained low (Fig. 1 and 2). Before fish removal, ~80% of charr were infected with ~8 *D. dendriticus* individuals. By 1987-1988, 40% of charr were infected with ~2 *D. dendriticus*

individuals (Table S1), although a few fish with more than 100 parasites were still present (Fig. 1 and 2). The variation in intensities decreased throughout the study period (Fig. 1 and 2). During the last 10 years, only a few infected fish were caught each year, typically with low infections. By 2016, we found no charr with *D. dendriticus*. The overlapping breakpoints between charr density and *D. dendriticus* prevalence and intensity (Table S2) correspond to the fish removal period and substantiates the rapid response of *D. dendriticus* to culling.

The long-term trends in infection with *D. ditremus* differed from *D. dendriticus*, with a slower and more oscillating decrease in both prevalence and intensity from the early 1990s to the end of the study period (Fig. 1 and 2). *Dibothriocephalus ditremus* prevalence was ~ 90% in the 1980s, thereafter slowly decreasing (Table S1). Prevalence was below 70% from 2007 to the end of the study, with a minimum 32% in 2009. The median intensity increased from ~15 in 1980-1981 to around ~20 in 1987-1988. From 1992 and onwards, intensity decreased, with the exception of 1999. From 2002 until 2016, the intensity was below 8 worms per infected fish. The breakpoint analysis did not define two significant temporal linear trends as seen for *D. dendriticus*.

Infection rate

Dibothriocephalus dendriticus infection rates declined after culling (Fig. 3). The age at which half the charr were infected also increased throughout the study period (Fig. 3). Before the fish removal, half the charr were infected by 2- (95% confidence interval: 1.6 – 2.6) years (Fig. 3). By 1987 – 1988, half the charr were infected by 5.7 (4.9 – 6.6) years increasing to 11.3 (10.4 – 12.3) years in the final period, i.e., 2011 – 2016. For *D. ditremus* the change in infection rates after culling was less clear (Fig. 3). Before the fish culling, half the charr were infected by 2.6 (2.2 – 3.2) years (Fig. 3). This decreased to 1.9 (1.7 – 2.3) years in 1987-88. By 2001-2005 half

274 the charr were infected by 3.1 (2.7 – 3.6) years, whereas at the study's end, half the charr were
275 infected by 4.3 (3.3 – 5.3) years.
276
277 *Parasite population size*
278 The tapeworm component population (i.e., total tapeworms in the charr population rather than
279 per fish) in Arctic charr declined exponentially after culling (Fig. 4). In the last ~10 years of the
280 study, the *D. ditremus* population had declined 7-10-fold and the *D. dendriticus* population
281 declined 20-60- fold compared to pre-culling years (Fig. 4).
282
283 **Are long-term trends in prevalence and intensity governed by charr density, demography**
284 **or brown trout density?**
285 The effect of the predictors *charr age, charr length, charr density* and *trout density* on parasite
286 prevalence and intensity differed between the two parasite species (Table S3). For *D.*
287 *dendriticus*, prevalence was positively associated with charr age ($F_{1,33}$ = 24.0, p < 0.001, slope
288 = 8.05 ± 1.64 s.e.) and charr density ($F_{1,33}$ = 10.4, p = 0.003, slope = 0.65 ± 0.20), but negatively
289 associated with trout density ($F_{1,33}$ = 38.7, p < 0.001, slope = -17.30 ± 2.78) (model r^2 = 0.86;
290 Table S3). Similarly, *D. dendriticus* intensity was positively associated with charr age ($F_{1,33}$ =
291 44.7, p < 0.001, slope = 1.39 ± 0.21) and charr density ($F_{1,33}$ = 23.9, p < 0.001, slope = 0.11 ±
292 0.02), but was negatively associated with charr length ($F_{1,33}$ = 30.1, P < 0.001, slope = -0.04 ±
293 0.01) (full model r^2 = 0.86; Table S3). For *D. ditremus*, neither prevalence nor intensity were
294 associated with charr density. *Dibothriocephalus ditremus* prevalence was negatively
295 associated with trout density ($F_{1,34}$ = 111.4, p < 0.001, slope = -23.11 ± 2.19) and positively
296 associated with charr length ($F_{1,34}$ = 27.7, p < 0.001, slope = 0.32 ± 0.06) (model r^2 = 0.77; Table
297 S3). The splined data for *D. ditremus* intensity created a bell-shaped curve from 1980-1981 to
298 1987-1988 that prevented the autocorrelation structure from being correctly modelled, even

when imposing both autoregressive and moving average terms. When excluding the first 10 years from the analysis, the model fit improved (AIC dropped from 56.4 to 45.2). *Dibothriocephalus ditremus* intensity was negatively associated with trout density ($F_{1,25} = 14.5$, $p < 0.001$, slope = -0.71 ± 0.19), and positively associated with charr age ($F_{1,25} = 17.5$, $p < 0.001$, slope = 0.42 ± 0.10) (model $r^2 = 0.69$).

Discussion

After fish culling, tapeworm prevalence and intensity declined. *Dibothriocephalus dendriticus* declined faster than did *D. ditremus* in response to the charr removal, presumably because the latter tapeworm maintained transmission to birds using the unfished sticklebacks as hosts (Kuhn et al., 2015). The vast decline in *D. dendriticus* was more affected by reduced charr age than reduced charr density, indicating that parasite mortality was more important than parasite transmission for this species.

Parasite intensity typically increases with fish age and length (Cardon et al., 2011; Poulin, 2000; Zelmer & Arai, 1998). *Dibothriocephalus* plerocercoids can live for several years in charr, resulting in older fish individuals accumulating higher infections (Halvorsen & Andersen, 1984; Henricson, 1977; Henriksen et al., 2016). When culling increases host mortality, age distributions can favour younger fish, as seen for fisheries (Berkeley, Hixon, Larson, & Love, 2004), resulting in fewer accumulated parasites. This appears to be the case in the present study, as *Dibothriocephalus* spp. infection per fish decreased following a demographic shift from old to young fish. For *D. dendriticus*, infection rates also declined, as measured by the increased age at which half the fish were infected.

Interestingly, even as charr declined, *D. ditremus* infection rates did not decrease, indicating that young charr were subject to the same infection pressure from *D. ditremus* as before. This parasite might have been able to persist by infecting sticklebacks (Kuhn et al., 2015). Red-breasted mergansers, the final hosts of *D. ditremus*, tripled in abundance from 1983 to 1992, probably in response to increases in stickleback numbers (Klemetsen et al., 2002; Klemetsen & Knudsen, 2013) that red-breasted mergansers prefer to eat (Gardarsson & Einarsson, 2002). The unexpected initial increase in *D. ditremus* per charr could also have been caused by increased consumption rates on copepods or sticklebacks in the remaining charr (Amundsen, 1989, 1994; Amundsen et al., 2007). The density of copepods did not change notably the first years following fish culling (Dahl-Hansen, 1995).

The *D. ditremus* population eventually declined as the abundance of large brown trout began to increase. Predation from the increasing trout population probably reduced the stickleback population, which would reduce *D. ditremus* transmission to birds. Furthermore, large trout accumulate tapeworm larvae as they prey on sticklebacks and charr (Henriksen et al., 2016; Knudsen, Klemetsen, & Staldvik, 1996), but likely act as sinks (Halvorsen, 1970), because they are too large for piscivorous birds to eat. *Dibothriocephalus* spp. in trout sampled between 2001 and 2011 from Takvatn showed that almost all were in trout > 35 cm (Henriksen et al., 2016). In addition, data from Takvatn suggests that *D. ditremus* transmission also declined due to a diet shift. The piscivory and cannibalism that normally leads to high infection rates in larger charr (Henriksen et al., 2016) declined as charr competed more with trout (Amundsen 1994; Eloranta et al., 2013). Furthermore, benthic prey such as snails and amphipods increased in the lake, allowing for a shift towards a more benthic diet in charr (Amundsen, 1989; Klemetsen, Knudsen, Staldvik, & Amundsen, 2003). Simultaneously, there was a habitat shift in small charr from the profundal and pelagic to the littoral (Klemetsen et al., 2002; Klemetsen, Muladal, &

Amundsen, 1992). Taken together, these results indicate a reduction in the feeding rates on the pelagic copepods that are the first intermediate hosts for *Dibothriocephalus* (Curtis, Bérubé, & Stenzel, 1995; Knudsen, Curtis, & Kristoffersen, 2004; Knudsen, Amundsen, Nilsen, Kristoffersen, & Klemetsen, 2008) as seen for European whitefish (*Coregonus lavaretus*) and brook charr (*Salvelinus fontinalis*) (Amundsen & Kristoffersen, 1990; Curtis, 1995). Ironically, this diet switch to the benthic amphipod *Gammarus lacustris* (Klemetsen et al., 2002) subjected charr to the *Gammarus*-transmitted nematode *Cystidicola farionis* (Knudsen, Kristoffersen, & Amundsen, 1999; Knudsen, Amundsen, & Klemetsen, 2002). This further points to how complex food webs can interact with fishing to alter the structure of parasite communities.

Culling hosts to reduce disease has been applied as a management strategy in terrestrial ecosystems (e.g. Harrison, Newey, Gilbert, Haydon, & Thirgood, 2010; Wasserberg, Osnas, Rolley, & Samuel, 2009; Woodroffe et al., 2006), but is rarely used to control fish parasites. Whether culling is a good management strategy depends on how long-lasting the effects are. Culling European whitefish only reduced parasite infection for a few years after fishing ended (Amundsen et al., 2002, 2018). In contrast, culling has reduced *Dibothriocephalus* spp. infection in the Takvatn charr population for more than three decades. We think tapeworms chiefly remain absent in Takvatn because the demographic shifts that resulted from culling (and increased parasite mortality and life cycle disruption) have persisted as the system shifted to a new stable state (Klemetsen et al., 2002, Persson et al., 2007, present study). In essence, the whole-lake experiment in Takvatn demonstrates that managing overcrowded fish populations by culling can produce two desirable outcomes; an increase in fish growth rates and reduced parasite burdens, effects that also should be reproducible elsewhere.

Authors' contributions

EHH, AMK, KDL, PAA, RoK and RuK conceived the ideas and designed methodology; EHH, PAA, Rok and RuK collected the data; EHH and AF analysed the data; EHH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data available via the Dryad Digital Repository. https://doi.org/10.5061/dryad.bd10668 (Henriksen et al., 2019).

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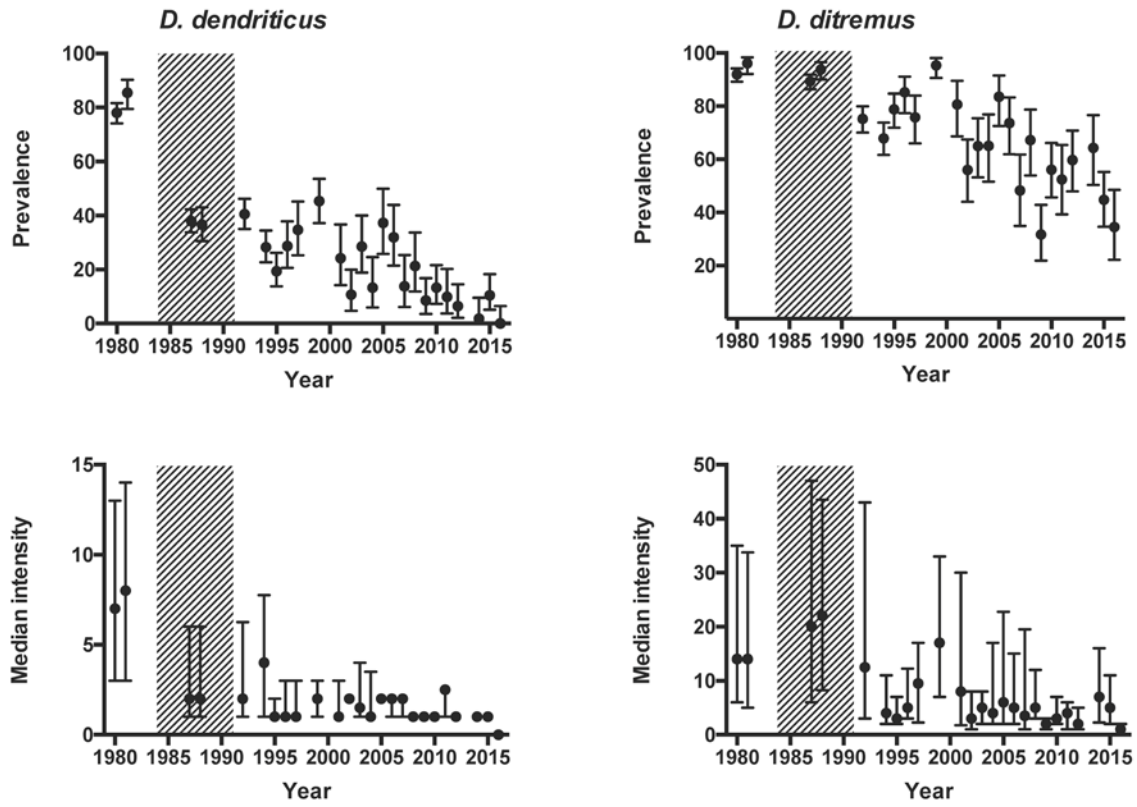
Figure legends

Fig. 1. Prevalence (top, with 95 % confidence intervals) and median intensity (bottom, with 25 and 75 percentiles) for *Dibothriocephalus dendriticus* (left) and *D. ditremus* (right) in Takvatn in years sampled. The hatched area indicates the culling period.

Fig. 2. Proportional distributions of Arctic charr with different abundances of *Dibothriocephalus dendriticus* (left) and *D. ditremus* (right) for six different time periods in Takvatn.

Fig. 3. Logistic regression showing the probability of infection with increasing charr age for *D. dendriticus* (a) and *D. ditremus* (b) during six different time periods in Takvatn between 1980 and 2016. The two graphs on the right side show the age (± 95% CI) at which 50 percent of the charr population become infected with *D. dendriticus* (c) and *D. ditremus* (d) for the different time periods.

Fig. 4. Estimated component population size of *Dibothriocephalus dendriticus* (grey lines, circles) and *D. ditremus* (black lines, squares) in Arctic charr from Takvatn.



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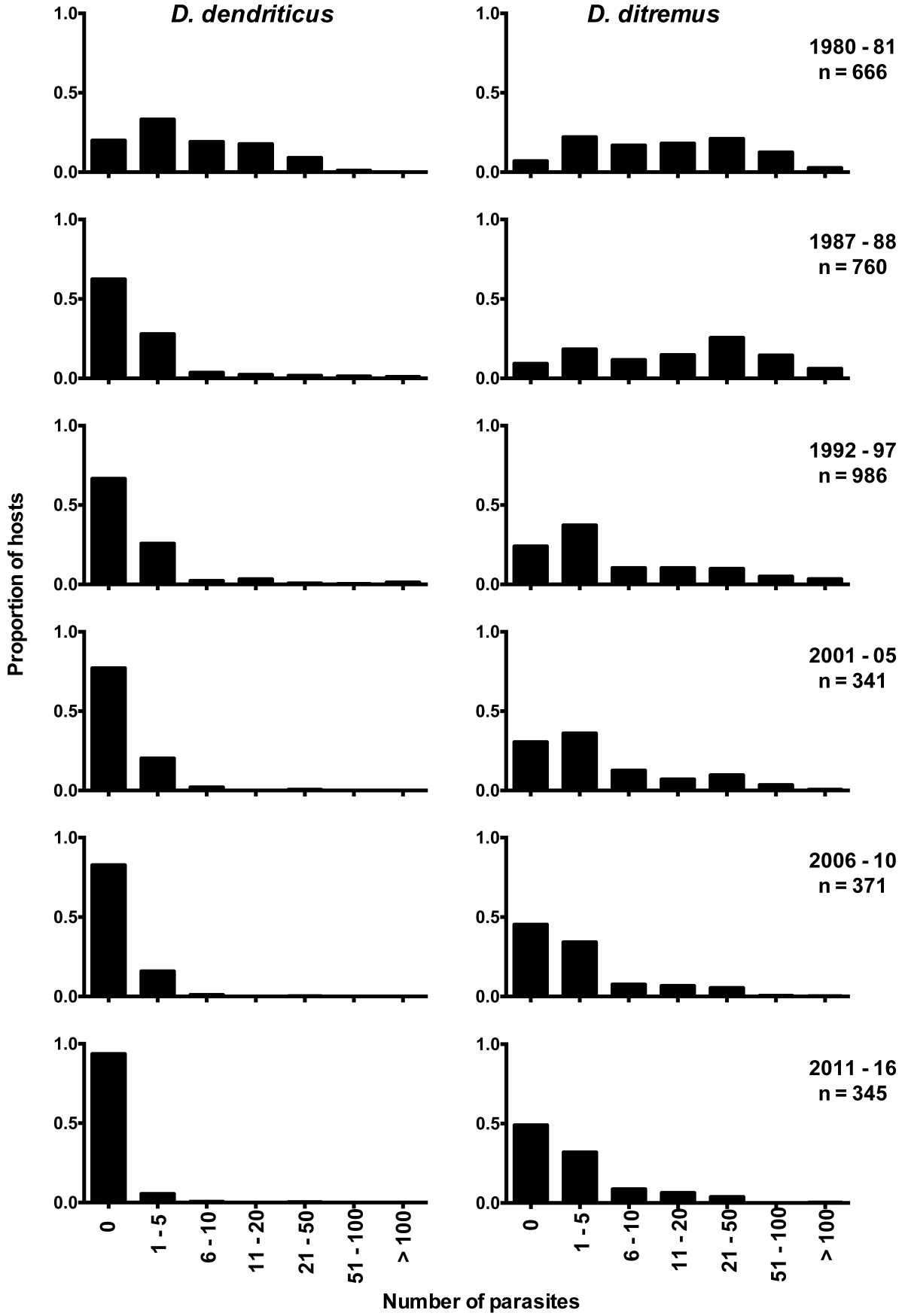
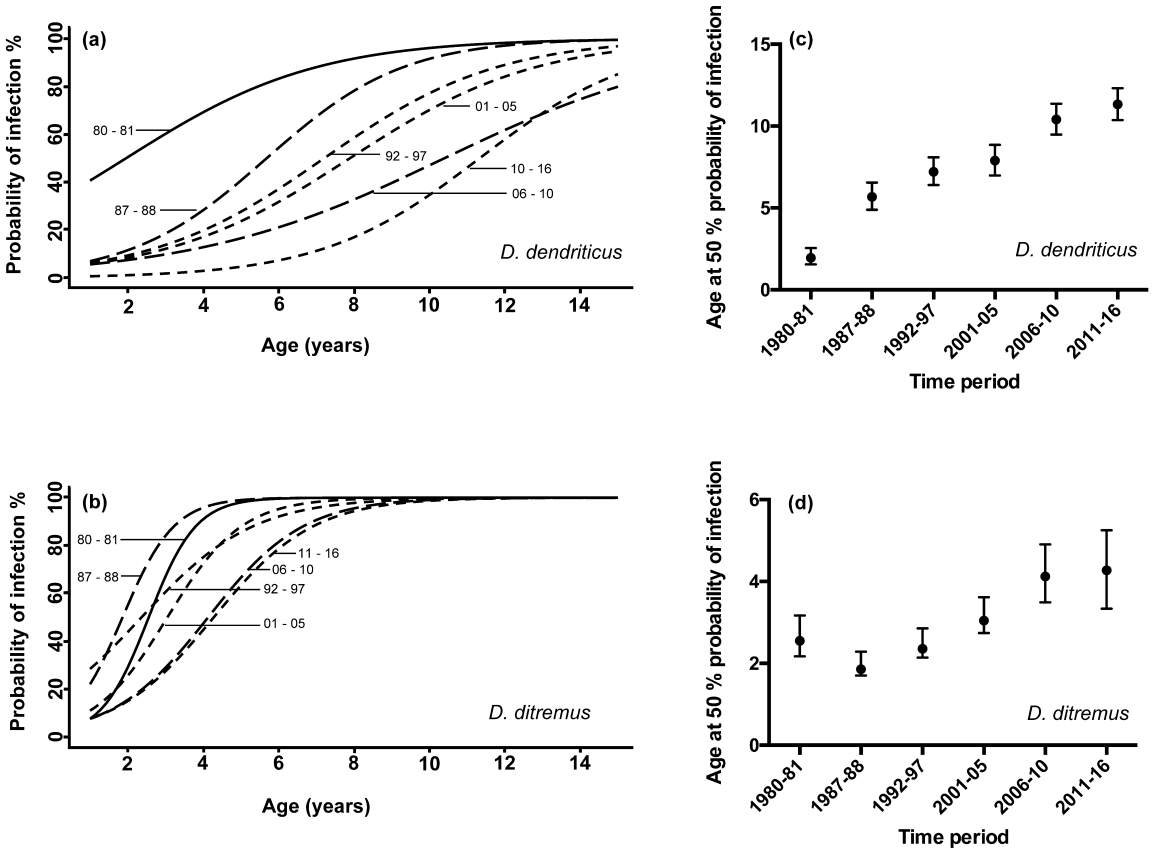
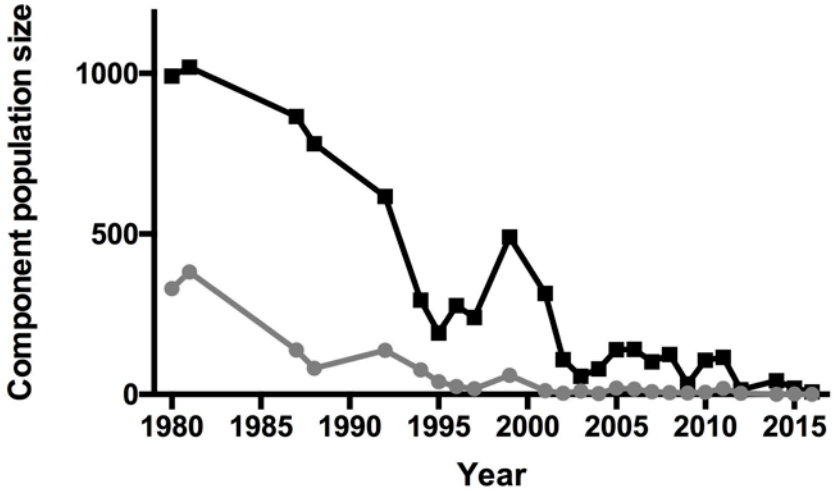

D. dendriticus
D. ditremus
1980 - 81
n = 666
1987 - 88
n = 760
1992 - 97
n = 986
2001 - 05
n = 341
2006 - 10
n = 371
2011 - 16
n = 345
Proportion of hosts
1.0
0.5
0.0
0
1 - 5
6 - 10
11 - 20
21 - 50
51 - 100
> 100
Number of parasites

643


(a)
Probability of infection %
Age (years)
80 - 81
87 - 88
92 - 97
01 - 05
10 - 16
06 - 10
D. dendriticus
(b)
Probability of infection %
Age (years)
80 - 81
87 - 88
11 - 16
06 - 10
92 - 97
01 - 05
D. ditremus
(c)
Age at 50 % probability of infection
Time period
1980-81
1987-88
1992-97
2001-05
2006-10
2011-16
D. dendriticus
(d)
Age at 50 % probability of infection
Time period
1980-81
1987-88
1992-97
2001-05
2006-10
2011-16
D. ditremus


Component population size
1000
500
0
1980
1985
1990
1995
2000
2005
2010
2015
Year

692 **Supplementary table 1.** Summary statistics of charr sampled for the present study. Number
693 of charr (N) and their mean age and length. CPUE (catch per unit effort) of charr and trout in
694 Takvatn. P = prevalence, MA = mean abundance, MI = median intensity, Var/mean =
695 variance of abundance divided by mean abundance for *Dibothriocephalus dendriticus* and *D.*
696 *ditremus*.
697

Year	N	Age	Length	CPUE charr	CPUE trout	*Dibothriocephalus dendriticus*				*Dibothriocephalus ditremus*			
						P	MA	MI	Var/mean	P	MA	MI	Var/mean
1980	478	5.8 ± 2.3	171 ± 28.3	43.1	0	78.0	7.7 ± 0.5	7	12.9	92.0	23.0 ± 1.3	14	33.6
1981	179	6.5 ± 4.5	179 ± 28.1	43.1	0	85.5	8.8 ± 0.7	8	9.9	96.1	23.7 ± 2.1	14	34.9
1987	516	4,5 ± 2.0	173 ± 53.3	25.7	0	38.0	5.4 ± 1.7	2	285.2	91.9	33.7 ± 2.8	20	117.7
1988	243	5.2 ± 2.2	191 ± 65.4	20.6	0	36.6	4.0 ± 1.1	2	74.4	93.8	37.9 ± 3.8	22	92.9
1992	311	6.5 ± 3.3	234 ± 106.4	20.1	2.7	40.5	6.8 ± 1.9	2	164.1	75.2	30.7 ± 4.1	12.5	171.4
1994	240	5.1 ± 2.9	195 ± 87.0	28.9	3.3	28.3	2.7 ± 0.8	4	49.9	67.9	10.1 ± 1.6	4	96.9
1995	170	3.5 ± 1.9	207 ± 62.4	34.6	3.0	19.4	1.1 ± 0.5	1	28.7	78.8	5.5 ± 1.0	3	13.8
1996	115	4.0 ± 1.4	227 ± 35.0	32.4	2.7	28.7	0.8 ± 0.2	1	6.5	85.2	8.5 ± 1.1	5	14.5
1997	95	3.9 ± 1.7	209 ± 58.9	25.9	1.5	34.7	0.7 ± 0.1	1	2.2	75.8	9.3 ± 1.3	9.5	13.2
1999	150	5.8 ± 1.6	237 ± 71.7	20.7	2.1	45.3	2.9 ± 1.1	2	65.6	95.3	23.7 ± 2.3	17	31.7
2001	62	5.3 ± 2.1	212 ± 88.1	20.2	3.3	24.2	0.6 ± 0.2	1	3.0	80.6	15.6 ± 3.2	8	40.8
2002	75	4.2 ± 1.9	178 ± 52.7	23.5	2.5	10.7	0.2 ± 0.1	2	3.2	56.0	4.6 ± 1.4	3	30.7
2003	77	4.2 ± 1.8	178 ± 56.9	13.8	2.2	28.6	0.7 ± 0.2	1.5	3.1	64.9	4.1 ± 0.7	5	8.6
2004	60	4.5 ± 1.8	190 ± 59.9	8.5	5.0	13.3	0.3 ± 0.1	1	3.3	65.0	9.3 ± 2.3	4	33.8
2005	67	4.8 ± 2.0	211 ± 86.9	11.1	2.7	37.3	1.7 ± 0.8	2	22.8	83.6	12.6 ± 2.1	6	23.8
2006	72	4.6 ± 1.8	184 ± 66.1	15.4	3.0	31.9	1.1 ± 0.4	2	8.9	73.6	9.1 ± 2.0	5	32.4
2007	58	4.5 ± 1.9	174 ± 54.5	20.4	2.2	13.8	0.4 ± 0.2	2	5.0	48.3	5.0 ± 1.3	3.5	20.3
2008	61	5.5 ± 2.6	223 ± 83.0	17.6	4.4	21.3	0.3 ± 0.1	1	1.4	67.2	7.0 ± 1.6	5	22.9
2009	82	3.8 ± 1.3	174 ± 49.7	33.0	12.6	8.5	0.1 ± 0.1	1	1.9	31.7	1.0 ± 0.3	2	6.3
2010	98	5.3 ± 2.3	245 ± 88.9	26.0	7.6	13.3	0.3 ± 0.1	1	2.3	56.1	4.1 ± 0.9	3	18.0
2011	61	4.8 ± 1.8	219 ± 67.0	25.0	9.5	9.8	0.7 ± 0.5	2.5	24.4	52.5	4.6 ± 1.8	4	44.9
2012	77	5.1 ± 1.8	247 ± 63.2	20.7	5.3	6.5	0.6 ± 0.4	1	1.3	59.7	2.4 ± 0.5	2	7.8
2014	56	4.3 ± 2.2	225 ± 91.5	19.9	8.2	1.8	0.0 ± 0.0	1	1.0	64.3	6.7 ± 1.3	7	14.6
2015	96	5.5 ± 2.7	237 ± 98.2	19.6	5.4	10.4	0.3 ± 0.1	1	5.7	44.8	3.5 ± 0.6	5	11.1
2016	55	3.5 ± 1.3	160 ± 45.8	14.0	5.3	0	0	-	0	34.5	1.5 ± 0.7	1	19.2

Supplementary table 2. Results from breakpoint analysis with breakpoints (year) provided as well as the slopes of the two linear trends on each side of the breakpoint.

Parameter	**Breakpoint (SE)**	**Slope 1 (95% CI)**	**Slope 2 (95% CI)**
Prevalence *D. dendriticus*	1987,0 (1.5), R^2 = 0.86	-6.58 (-3.22, -9.94)	-1.31 (-0.93, -1.68)
Median intensity *D. dendriticus*	1987.2 (0.9), R^2 = 0.79	-0.89 (-0.59, -1.20)	-0.04 (-0.08, 0.00)
Prevalence *D. ditremus*	2014.3 (1.6), R^2 = 0.62	-1.17 (-1.54, -0.80)	-13.69 (-45.10, 17.72)
Median intensity *D. ditremus*	1986.2 (2.7), R^2 = 0.62	0.66 (-0.92, 2.23)	-0.58 (-0.75, -0.40)

Supplementary table 3. Results from GLS models predicting *Dibothriocephalus dendriticus* and *D. ditremus* prevalence and intensity following model selection using AIC. Autoregressive (AR) or moving average (MA) correlation fitted to models where needed.

Repsonse variable	Model summary	Predictor	Coef ± s.e.	F value	P-value
Dibothriocephalus dendriticus prevalence	full model r^2 = 0.86, Correlation structure: ARMA (0, 1), theta = 0.75, Residual standard error: 8.89 Degrees of freedom: 37 total; 33 residual	Intercept	-3.88 ± 12.96		
		Log (trout CPUE +1)	-17.30 ± 2.78	38.68	<0.001
		Charr CPUE	0.65 ± 0.20	10.42	0.003
		Age	8.05 ± 1.64	24.00	<0.001
Dibothriocephalus dendriticus intensity	full model r^2 = 0.86, Correlation structure: ARMA (0, 1), theta = 0.69, Residual standard error: 0.86 Degrees of freedom: 37 total; 33 residual	Intercept	0.44 ± 1.34		
		Charr CPUE	0.11 ± 0.02	23.95	<0.001
		Length	-0.04 ± 0.01	30.13	<0.001
		Age	1.39 ± 0.21	44.66	<0.001
Dibothriocephalus ditremus prevalence	full model r^2 = 0.77, Correlation structure: ARMA (0, 0), Residual standard error: 8.84 Degrees of freedom: 37 total; 34 residual	Intercept	36.12 ± 11.53		
		Log (trout CPUE +1)	-23.11 ± 2.19	111.42	<0.001
		Length	0.32 ± 0.06	27.7	<0.001
log (*Dibothriocephalus ditremus* intensity)	full model r^2 = 0.69, Correlation structure: ARMA (1,1), phi = -0.17, theta = 0.49 Residual standard error: 0.45 Degrees of freedom: 28 total; 25 residual	Intercept	0.75 ± 0.65		
		Age	0.42 ± 0.10	17.47	<0.001
		Log (trout CPUE +1)	-0.71± 0.19	14.46	<0.001

Supplementary table 4. Summary for logistic regression models of probability of infection with *Dibothriocephalus dendriticus* probability of infection vs Arctic charr age for individual years. For some years, regressions were not fit due to the intercept or age-coefficient not being significant, thereby causing poor model fit. Asterisks indicate levels of significance (*, $P < 0.05$, **, $P < 0.01$, *** $P < 0$). NS = not significant.

Year	Intercept (***)	Age (***)	Z-value intercept	Z-value age	Degrees of freedom	Age at 50 % maturation
1980	-0.89 ± 0.33 **	0.41 ± 0.06 ***	-2.69	6.35	486	2.2
1981	NS					
1987	-3.22 ± 0.31 ***	0.60 ± 0.07 ***	-10.25	9.02	515	5.3
1988	-3.27 ± 0.46 ***	0.52 ± 0.08 ***	-7.06	6.13	237	6.3
1992	-3.64 ± 0.42 ***	0.49 ± 0.06 ***	-8.71	8.54	269	7.4
1994	-3.39 ± 0.42 ***	0.43 ± 0.06 ***	-8.03	6.69	226	7.8
1995	-3.62 ± 0.64 ***	0.50 ± 0.14 ***	-5.62	3.54	113	7.3
1996	-3.28 ± 0.81 ***	0.56 ± 0.19 **	-4.06	2.98	112	5.8
1997	-2.76 ± 0.73 ***	0.51 ± 0.17 **	-3.80	3.09	86	5.4
1999	-3.72 ± 0.82 ***	0.61 ± 0.14 ***	-4.52	4.49	144	6.1
2001	-4.13 ± 1.16 ***	0.51 ± 0.18 **	-3.56	2.90	60	8.0
2002	-4.93 ± 1.20 ***	0.56 ± 0.20 **	-4.11	2.85	74	8.8
2003	-2.49 ± 0.75 ***	0.34 ± 0.15 *	-3.34	2.24	73	7.4
2004	-4.66 ± 1.29 ***	0.58 ± 0.22 **	-3.61	2.64	51	8.0
2005	-1.91 ± 0.72 **	0.30 ± 0.14 *	-2.65	2.21	63	6.4
2006		NS				
2007	-4.76 ± 1.43 ***	0.56 ± 0.24 *	-3.33	2.36	51	8.5
2008		NS				
2009	-5.68 ± 1.58 ***	0.70 ± 0.30 *	-3.60	2.30	75	8.1
2010	-5.55 ± 1.19 ***	0.59 ± 0.16 ***	-4.66	3.67	93	9.4
2011	-5.90 ± 1.95 **	0.68 ± 0.31 *	-3.02	2.16	47	8.7
2012	-5.33 ± 1.58 ***	0.47 ± 0.23 *	-3.37	2.04	71	11.3
2014		NS				
2015	-4.80 ± 1.15 ***	0.41 ± 0.14 **	-4.18	2.85	84	11.8
2016	NS	NS				

Supplementary table 5. Summary for logistic regression models of probability of infection with *Dibothriocephalus ditremus* probability of infection vs charr age for individual years. For some years, regressions were not fit due to the intercept or age-coefficient not being significant, thereby causing poor model fit. Asterisks indicate levels of significance (*, P < 0.05, **, P < 0.01, *** P < 0). NS = not significant.

Year	Intercept (***)	Age (***)	Z-value intercept	Z-value age	Degrees of freedom	Age at 50 % maturation
1980	-3.73 ± 0.78 ***	1.51 ± 0.23 ***	-4.75	6.65	486	2.5
1981	-7.81 ± 2.87 **	2.50 ± 0.77 **	-2.72	3.26	178	3.1
1987	-2.75 ± 0.54 ***	1.47 ± 0.18 ***	-5.01	8.06	515	1.9
1988	-2.56 ± 1.00 *	1.43 ± 0.32 ***	-2.56	4.51	237	1.8
1992	-3.85 ± 0.79 ***	1.11 ± 0.21 ***	-4.87	5.35	269	3.5
1994	-1.34 ± 0.35 ***	0.48 ± 0.08 ***	-3.82	5.70	226	2.8
1995	-3.50 ± 1.14 **	1.63 ± 0.43 ***	-3.07	3.81	113	2.1
1996	-5.21 ± 1.72 **	2.03 ± 0.54 ***	-3.03	3.80	112	2.6
1997	-2.01 ± 0.80 *	0.95 ± 0.25 ***	-2.52	3.77	86	2.1
1999	NS					
2001	-4.63 ± 1.60 **	1.50 ± 0.46 ***	-2.89	3.29	60	3.1
2002	-3.13 ± 0.91 ***	0.86 ± 0.24 ***	-3.43	3.56	74	3.6
2003	-4.09 ± 1.08 ***	1.24 ± 0.29 ***	-3.80	4.22	73	3.3
2004	-2.45 ± 1.18 *	0.88 ± 0.32 **	-2.07	2.78	51	2.8
2005	NS					
2006	NS					
2007	-3.12 ± 0.98 **	0.66 ± 0.21 **	-3.18	3.17	51	4.7
2008	-4.67 ± 1.46 **	1.20 ± 0.34 ***	-3.21	3.55	59	3.9
2009	-4.55 ± 1.06 ***	0.97 ± 0.26 ***	-4.30	3.72	75	4.7
2010	-3.54 ± 0.82 ***	0.78 ± 0.17 ***	-4.30	4.51	93	4.6
2011	-5.65 ± 1.81 **	0.68 ± 0.31 ***	-3.12	3.47	47	4.1
2012	-2.64 ± 0.97 **	1.37 ± 0.40 **	-2.73	3.13	71	4.1
2014	-2.48 ± 0.82 **	0.78 ± 0.21 ***	-3.02	3.70	53	3.2
2015	-4.57 ± 0.92 ***	0.86 ± 0.18 ***	4.96	4.91	84	5.3
2016		NS				