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Long-term dynamics of metazoan parasites in an age- and size-structured host population

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“Science is a social endeavor”

UiT Freshwater Ecology Group motto

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Summary

Parasites negatively affect hosts and may constitute serious management problems. At the same time, parasites are integral components of ecosystems and represent a substantial part of the biodiversity on earth. Understanding the ecological factors that influence the abundance and distribution of parasite populations is therefore important from a management perspective, but also to understand the mechanisms that shape populations and food webs. Parasites occur in complex food webs, with several opportunities for indirect effects. Ecosystem perturbations have been key to identify ecological processes that influence population and community dynamics. As some of these processes take a long time to unfold, they are only detectable from long-term studies. Unfortunately, few long-term studies have investigated host-parasite dynamics. The main aim of this thesis was to study how temporal changes in density and age- and size-structure of Arctic charr (*Salvelinus alpinus*) as a host species affected metazoan parasite dynamics across more than three decades of field observations from a subarctic lake. I also investigated the effects of the density of a competitor and predator, brown trout (*Salmo trutta*), on parasite abundance in the focal host Arctic charr.

I documented that experimentally reducing the density of Arctic charr through culling reduced the prevalence and intensity of two trophically transmitted *Dibothriocephalus* tapeworm species. The decline in the parasite infections was mainly due to culling-induced changes in host population age structure and increased predation rates from brown trout. Furthermore, I found that changes in host body size explained most of the variation in the dynamics of *Salmincola edwardsii* gill lice, a directly transmitted copepod parasite. In this case, the density of brown trout surprisingly amplified transmission rates to Arctic charr. Finally, the abundance

and aggregation of the long-lived swimbladder nematode *Cystidicola farionis* was chiefly driven by host-population age structure. As host age increased, so did parasite abundance, which in turn reduced parasite aggregation. Heterogeneity in feeding and body size further increased aggregation, but stratifying the data by age diminished this effect. Accordingly, the relative composition of age classes each year determined the abundance and distribution of this parasite among the charr hosts.

Combining my results with detailed long-term studies on the free-living community in the lake allowed me to identify some key parameters that structure the long-term dynamics of three metazoan parasite taxa with contrasting life cycles. The inverse relationship between fish population density and individual consumption rates led to increases in somatic growth and fish body size as the density of Arctic charr decreased. This shifted the predominant size distribution of the host population from a zooplankivorous to a benthivorous ontogenetic stage, leading to a shift in parasite exposure from *Dibothriocephalus* spp to *Cystidicola farionis*. Furthermore, the reductions in Arctic charr density affected size-structured interactions with brown trout thereby increasing brown trout density, which both reduced (*Dibothriocephalus*) and facilitated (*Salmincola*) parasite transmission to Arctic charr.

In fish population ecology, size-structured population models highlight the strong link between ontogenetic development and population and community dynamics. These processes feedback to shape size distributions and individual fish behaviors. In this thesis, I show that such mechanisms also are crucial in shaping long-term parasite dynamics, but that the direction of effects vary depending on the parasite species and life cycle involved.

List of papers

Paper I

Eirik H. Henriksen, André Frainer, Rune Knudsen, Roar Kristoffersen, Armand M. Kuris, Kevin D. Lafferty, & Per-Arne Amundsen. 2019. Fish culling reduces tapeworm burden in Arctic charr by increasing parasite mortality rather than by reducing density-dependent transmission. Journal of Applied Ecology, 56(6), pp. 1482-1491. doi: 10.1111/1365-2664.13369

Paper II

Eirik H. Henriksen, André Frainer, Robert Poulin, Rune Knudsen, & Per-Arne Amundsen. Long-term ectoparasite population dynamics driven by changes in host size but not host density or temperature. Manuscript.

Paper III

Eirik H. Henriksen, André Frainer, Rune Knudsen, & Per-Arne Amundsen. Fish age and population size structure affect the abundance and aggregation of a long-lived nematode parasite. Manuscript

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	EHH, AF, AMK, KDL, PAA, RoK, RuK	EHH, RP	EHH
Study design, data gathering and methods	EHH, PAA, RoK, RuK	EHH, PAA, RuK	EHH, PAA, RuK
Data analyses and interpretation	EHH, AF, KDL	EHH, AF, RP	EHH
Manuscript preparation	EHH, AF, AMK, KDL, PAA, RoK, RuK	EHH, AF, RuK, RP, PAA	EHH, AF, PAA, RuK

Authors: Eirik Haugstvedt Henriksen (EHH), Per-Arne Amundsen (PAA), Roar Kristoffersen (RoK), Rune Knudsen (RuK), André Frainer (AF), Armand M. Kuris (AMK), Kevin D. Lafferty (KDL) and Robert Poulin (RP)

Preamble

The present thesis addresses long-term dynamics in the parasite infections of Arctic charr, *Salvelinus alpinus*, and attempts to identify key ecological drivers explaining temporal variations and distributional patterns revealed for three parasite taxa with contrasting life cycles. Metazoan parasites have life cycles that range from relatively simple and direct, involving a single host species, to complex life cycles with multiple obligate hosts. The three parasite taxa represent the spectrum of life cycle complexity, from a direct life cycle with Arctic charr as the single host, to complex cycles with a multitude of hosts at each developmental stage of the parasite (Figure 1). Whereas each paper deals with a specific host-parasite association, the goal of this synopsis is to integrate the findings from the three papers and point to commonalities and differences across my results. I begin by introducing some aspects of parasite population ecology.

Introduction

Population ecologists try to understand the distribution and abundance of organisms over space and time (Begon et al. 2014). Whereas some animal populations are spatially distinct and easy to define, many exist as metapopulations consisting of subpopulations that occupy distinct resource patches (Levins 1969; Hanski and Gilpin 1991; Begon et al. 2014). The local dynamics of individuals within each subpopulation determine the overall dynamics of the metapopulation. This is evident for parasite populations which are nested within different levels of their host population(s) (Bush et al. 1997). Each host individual harbors an infrapopulation of parasites, each host population harbors a component population of parasites, and the sum of all parasite individuals across all host populations, including free-living stages of the parasite, make up the parasite suprapopulation (Bush et al. 1997). The regulation of a parasite suprapopulation is the sum of processes operating on all parasite stages across all hosts (Poulin 2007). Due to the complexity of studying a parasite suprapopulation, population studies on parasites typically focus on the component population level by examining individual infrapopulations.

Within a host population, some hosts harbor a disproportionately large number of the parasite population. This aggregated distribution of parasites is ubiquitous across host-parasite systems (Shaw and Dobson 1995; Poulin 2013). What generates this heterogeneity among parasite infrapopulations? Said in other words, why are some hosts more infected with parasites than others are? Several host attributes can influence its suitability as a habitat for parasites. Two important parameters are behavior and immunity that influence exposure and susceptibility to parasites, respectively (Daly and Johnson 2011; Barron et al. 2015). Differences in behavior among host individuals affecting habitat use or diet can reduce or increase parasite exposure, and efficient immune responses reduce parasite establishment post-exposure, i.e. decrease susceptibility. It can be difficult to separate the two mechanisms, as covariation between exposure to parasites and susceptibility to infection is difficult to detect, but likely widespread in natural populations (Hawley et al. 2011)**.** However, for fish, variation in exposure appears to be more important than variation in susceptibility for generating aggregated parasite distributions (Karvonen et al. 2004; Bandilla et al. 2005; Poulin 2007). Besides behavior, another intrinsic property of the host that affects both exposure and susceptibility to parasites is size. Larger hosts provide more space for parasite individuals and consume larger quantities of potential intermediate hosts (Poulin 2000). Further, host size correlates with host age, and larger hosts can therefore accumulate more parasites over time (Zelmer and Arai 1998). In sum, several mechanisms can generate heterogeneity in infection levels among host individuals. How does among-host variation in parasite exposure affect parasite population dynamics?

The processes that regulate the total number of parasites in a population operate at both the infrapopulation and the whole population level (Poulin 2007). New infrapopulations form when uninfected hosts become infected with parasites, and infrapopulations go extinct when their hosts die. Infrapopulations are therefore temporary entities with a continuous turnover. Changes at the component or suprapopulation levels track changes in the configuration of infrapopulations. Simple mathematical models show that long-term changes in parasite populations can be solely due to changes in the age and size-distribution of hosts, with infection pressure from the environment remaining constant (Des Clers 1991). Thus, changing the age- and size distribution of hosts will influence the size and composition of infrapopulations, with important implications for parasite population and disease dynamics (Des Clers 1991; Ben-Ami 2019).

Another important determinant of parasite component population size is host density. The total size of the component population equals mean abundance, i.e. the average abundance of parasite in infrapopulations, multiplied by the total number of hosts. Increasing the number of hosts increases the number of infrapopulations, thus increasing component population size if the infrapopulation size remains constant. Furthermore, the probability that an infective parasite transmission stage encounters a host increases with the density of hosts. Parasite transmission rates will therefore typically increase as a function of host density (Hopkins et al. 2020), which should lead to an increase in parasite abundance. However, parasite abundance can also decrease with host density due to encounter-dilution effects (Buck and Lutterschmidt 2017). In this scenario, increasing the density of hosts leads to fewer available parasites per host. Taken together, temporal changes in host behavior, demography (age and size distribution) and density all have the potential to affect parasite populations over time.

Besides the aforementioned host attributes affecting parasite populations, density-dependent mechanisms acting on the parasite infrapopulations have the potential to regulate parasite population dynamics. If regulatory mechanisms are operating, mathematical models predict that host and parasite populations attain equilibria and show predictable and stable levels (Anderson and May 1978). Some of these density-dependent mechanisms include reductions in parasite establishment rates, constraints on parasite population growth within individual hosts, and mortality of heavily infected hosts (Anderson and May 1978; Poulin 2007). Such regulation is easy to demonstrate in host-parasite models (e.g. Anderson and May 1978). Whereas laboratory studies have provided empirical evidence for density dependence regulating parasite populations, infrapopulations might under natural conditions not reach a large enough size for density-dependence to occur (Poulin 2007). The few long-term studies from parasites of freshwater fish suggest that there is little evidence that suggests that these parasite populations are regulated through density-dependent interactions (Kennedy 1977, 2009). Rather, long-term stability could just as easily result from stable physiochemical conditions (Kennedy 2009). In a broader context, although parasites might affect several properties of food webs (Lafferty et al. 2006, 2008), the structure and dynamics of food webs are also essential for the abundance and distribution of parasites (Marcogliese 2002). A stable food web could thus lead to stable transmission rates and stable parasite infection levels, without density-dependent constraints operating.

Fish are ideal model organisms to study several aspects of parasite population ecology. Each fish species typically host numerous parasite species from several different phyla (Hoffman 1999; Dobson et al. 2008), and it is relatively easy to collect adequate number of hosts for accurate estimates of host and parasite population parameters (Jovani and Tella 2006). Parasites are easily counted from individual hosts, and well-established methods exist for estimating fish age, size and densities (Schreck and Moyle 1990; Maunder et al. 2006). Lacustrine fish populations are particularly well suited for studying host-parasite dynamics, as lakes form distinct ecosystems with well-defined fish populations (Likens 2010). The fact that we can count parasite individuals in hosts from distinct populations within an ecosystem allows us to unravel mechanisms that structure parasites on the individual, population and community level of hosts (Kennedy 2009; Tompkins et al. 2011). There are certain aspects of fish population ecology that are key to consider when studying host-parasite dynamics in fishes.

Fish populations are typically size structured, and larger species often undergo ontogenetic niche shifts that change the character and strength of ecological interactions during their life cycle (Werner and Gilliam 1984; de Roos and Persson 2013). Feeding ecology and competitive and predatory interactions change with fish size with important implications for long-term population and community dynamics (Ebenman and Persson 1988; de Roos and Persson 2013). This has convincingly been shown in whole-lake perturbation experiments where the interplay between fish density, body size and ecological interactions shape long-term dynamics in fish communities (Byström et al. 1998; Post et al. 1999; Persson et al. 2007). The close association between parasite transmission and host characteristics like density, feeding ecology and body size suggests that size-structured interactions in fish should also affect parasite population dynamics. For instance, diet composition and consumption rates change with fish size (Amundsen et al. 2007; Sánchez-Hernández et al. 2019), with strong effects on the abundance and composition of trophically transmitted parasites (Henriksen et al. 2016; Prati et al. 2020). However, it is not clear how long-term interactions among fish density, feeding ecology, and age- and size-structure will affect parasite population dynamics. As an example, we might consider how increasing fish density might affect parasite populations. Increasing fish density should increase parasite transmission rates, but will simultaneously reduce individual fish size. The reductions in fish size will affect feeding ecology and competitive and predatory interactions. Predicting the outcome for the parasite population becomes difficult. In the present thesis, I examine how such interrelationships affect long-term dynamics of parasites in Arctic charr, a fish species that shows chief variation in somatic growth and size (Amundsen et al. 2007; Klemetsen 2013) and is known to undergo large ontogenetic niche shifts (Klemetsen et al. 2003; Prati et al. 2020).

Arctic charr host numerous metazoan parasite species, of which more than 10 are found in Takvatn (Kristoffersen 1993; Kuhn 2015; Soldánová et al. 2017). Since most of these parasites are food transmitted and Arctic charr show high among-individual variations in diet, feeding behaviour is one of the most important factors structuring parasite infrapopulations (Knudsen et al. 1996, 2004, 2008). Furthermore, ontogenetic dietary changes lead to shifts in parasite infrapopulations and communities with the size and age of charr (Henriksen et al. 2016; Prati et al. 2020), with parasite abundance typically increasing with fish size and age as for other fishes (Zelmer and Arai 1998; Poulin 2000). Arctic charr diet is in turn determined by prey availability, fish size and ecological interactions such as interspecific and intraspecific competition (Klemetsen et al. 2003; Amundsen et al. 2007). Individual Arctic charr tend to specialize on either benthic or pelagic prey items in lakes which expose them to different trophically parasite species (Knudsen et al. 2014). Temporal stability in the degree of individual specialization thus leads to stability in their community of parasites (Kuhn 2015).

Main research questions

The overall aim of this thesis was to study how abundance of metazoan parasites of Arctic charr in subarctic lake Takvatn changed across time, and identify the most important ecological drivers of this temporal variation in parasite populations. Takvatn has been the subject of numerous ecological studies over the past four decades. Many of them being related to a large-scale fish culling experiment carried out predominantly from 1984 to 1989, prior to which a dense population of small-sized Arctic charr dominated the fish community. During this whole-lake experiment, funnel traps were used to cull ~35 metric tons of Arctic charr, reducing charr density by ~80%. The fish removal led to vast changes in the density, size, age and diet of Arctic charr, and facilitated a comeback for the brown trout population which was nearly absent in the lake (Klemetsen et al. 2002; Amundsen et al. 2007, 2019; Persson et al. 2007). All these effects could influence the transmission of parasites to Arctic charr. Because of the detailed ecological knowledge of the long-term dynamics of the system, it is possible to posit specific hypotheses on how parasites with different life cycles would respond temporally. The three parasite taxa differ in their life cycles, ranging from simple to complex (Figure 1). The simplest life cycle belongs to *Salmincola edwardsii*, a parasitic copepod with a direct life cycle and a free-living infective copepodid stage. *Cystidicola farionis* is adult in the swimbladder of Arctic charr and transmits trophically with the amphipod *Gammarus lacustris* as its sole intermediate host. The most complex life cycles belong to two *Dibothriocephalus* species (*D. ditremus* and *D. dendriticus*) with a three-host life cycle, where copepods are the first intermediate host, several fish species are second intermediate and sometimes paratenic hosts, and birds are final hosts. Among the parasites infecting Takvatn charr, these four species are the ones for which the longest and most detailed time series have been collected. Importantly, they form the basis for nice comparisons due to their contrasting life cycles.

Overall question:

- How do changes in fish density, demography and ecology affect long-term dynamics of different metazoan parasites with contrasting life cycles?

Specifically I ask:

- How do temporal changes in fish age and size-structure affect parasite abundance in Arctic charr (**all three papers**)?

- Is there a direct effect of host density on transmission of parasites to Arctic charr? (**paper I and II**)
- How does fish culling affect parasite transmission to Arctic charr? (**paper I**)
- How do long-term changes in host age, parasite abundance and parasite aggregation interact? (**paper III**)

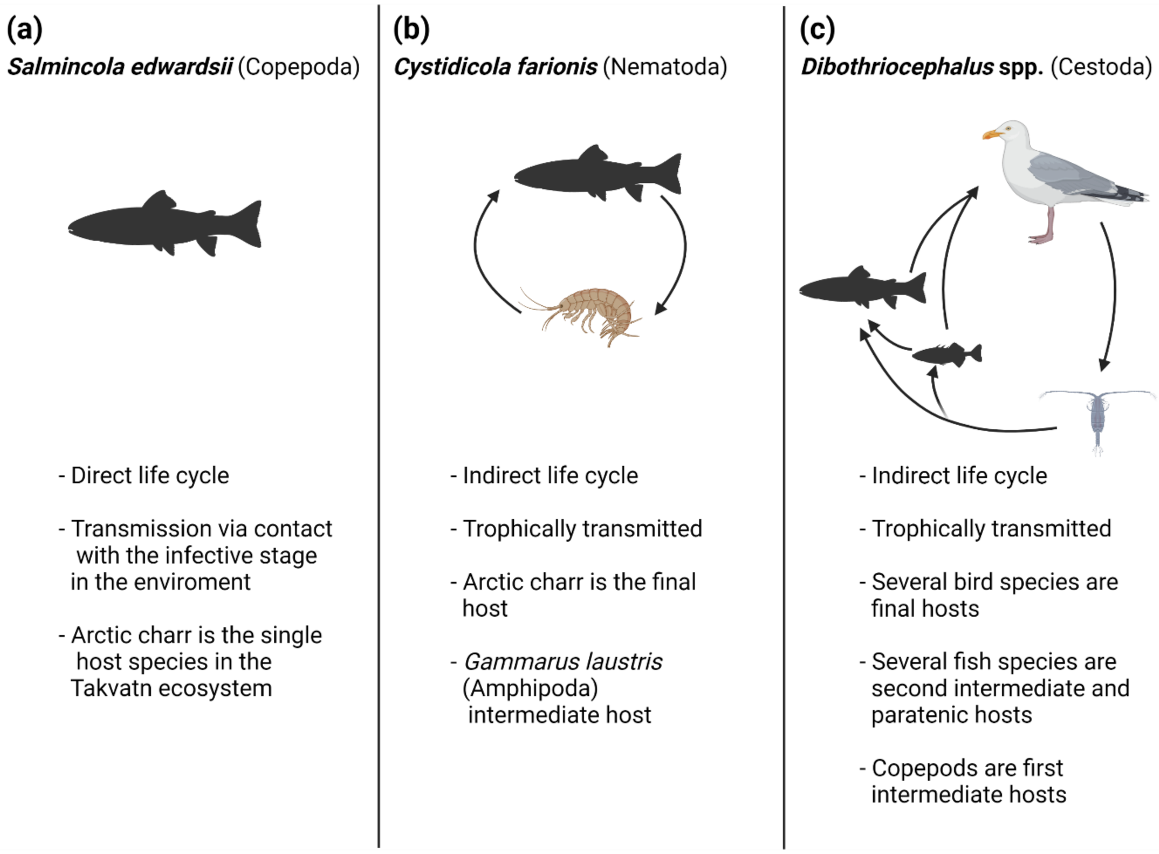

Figure 1. The life cycles of the parasite taxa studied in the present thesis. (a) *Salmincola edwardsii* is an ectoparasitic copepod with a direct life cycle. Adult female copepods release eggs into the water that hatch into free-living copepodids that infect other Arctic charr. (b) *Cystidicola farionis* is a parasitic nematode that infects the swimbladder of Arctic charr. Fish release eggs into the environment where they must be consumed by the amphipod *Gammarus lacustris*. Infected amphipods must then be consumed by Arctic charr for the parasite to complete its life cycle. (c) *Dibothriocephalus ditremus* and *D. dentriticus* are parasitic tapeworms that mainly use ducks and divers (*D. ditremus*), and gulls and terns (*D. dendriticus*) as final hosts. Eggs are released into the lake with bird feces that hatch into a coracidium, which is consumed by a copepod. Infected copepods are then consumed by fish. The parasite can further be transmitted from fish to fish via piscivory. In Takvatn, Arctic charr, brown trout and 3-spined sticklebacks are hosts to both *Dibothriocephalus* species. Infected fish must be consumed by birds for the parasite to complete its life cycle.

Materials and methods

Study system

Takvatn (suffix ‘vatn’ means ‘lake’) is a 15 km^2 large lake in Troms county, northern Norway (see paper 1 and references therein for specific information on the lake and its biota). The lake is oligotrophic and contains three fish species: Arctic charr, brown trout (*Salmo trutta*) and 3-spined sticklebacks (*Gasterosteus aculeatus*). Numerous ecological studies have been conducted at Takvatn dating back to 1980. At the time, there was no intention to start a long-term study that would last 40 years. Rather, many of the studies were conducted as separate master theses and PhD projects. Luckily for me, two of these studies included an extensive sampling of *Dibothriocephalus* spp. (at the time recognized as *Diphyllobothrium*) in 1980, 1981, 1987 and 1988 and *Cystidicola farionis* in 1987 and 1988 (Kristoffersen 1993; Knudsen 1997). Other studies investigated Arctic charr ecology and the composition of the zooplankton community in the lake (Amundsen 1989; Svenning 1993; Dahl-Hansen 1998). The outcomes from these studies generated new questions and hypotheses that were followed up by more studies which formed the basis for the long-term monitoring and sampling which has been conducted annually since the 1990s (Amundsen et al. 2019). Parasites were sampled somewhat sporadically in the early years, but have been included more or less annually over the past two decades. For this reason, some of the time series presented in this thesis have missing years, particularly in the beginning. However, as this early period constitutes a period of significant ecological change in the system, I have included all available years of data in the present study to investigate how the parasite populations have responded to these changes.

The fish removal experiment and its ecological consequences

A common theme to the early research conducted at Takvatn was a large-scale fish removal experiment that removed > 690 000 individual of Arctic charr from the lake between 1984 and 1991, with most fish being removed during the first years of this period. The effort was conducted as a means to improve the suitability of the Arctic charr to harvest, as small fish with high parasite burdens of *Dibothriocephalus* tapeworms dominated the overcrowded population. Since the only parasite species sampled prior to the fish removal experiment were the two *Dibothriocephalus* species, paper 1 is the only paper addressing the direct effects of the fish removal on parasite abundance. However, the effects of the perturbation on the Takvatn food web have echoed in the system for decades (Persson et al. 2007; Amundsen et al. 2019; Prati et al. 2021). Many of the changes in the system have happened as a domino effect of the fish removal, and some of them have the potential to affect all three parasite species in my thesis. The effects of the culling on the free-living community have been extensively covered. They include changes in the age and size structure of Arctic charr, from a population dominated by old slow-growing fish pre-culling to younger and larger fish from the late 1980s and onwards (Klemetsen et al. 2002). There was a shift in Arctic charr feeding as well, with increased consumption rates towards benthic prey and a smaller proportion of zooplankton and sticklebacks in Arctic charr diets (Amundsen et al. 2007, 2019; Prati et al. 2021). As Arctic charr density decreased, the brown trout population increased resulting in increased interspecific competition with brown trout for food and space, and increased predation rates from brown trout on small Arctic charr (Persson et al. 2007, 2013). Whereas the effects of the fish removal on Arctic charr growth rates was rapid (Amundsen et al. 1993), some of the community responses took decades to unfold (Amundsen et al. 2019). Hence, in all three papers, the effects of the fish culling echo through the time series.

Sampling method

Throughout the long-term studies at Takvatn gill nets with multiple mesh sizes ranging from 10 mm to 45 mm knot to knot have been used to sample the fish populations. Nets have been deployed in the littoral, pelagic and profundal zones of the lake, thus providing a sample of the whole population and its different ontogenetic stages. It is important, however, to note that this method tends to underrepresent the smallest (< 10 mm) and youngest (< 2 years) fish (Finstad et al. 2000). However, as these fish carry few, if any, parasites this should not affect the conclusions drawn in the different papers. I refer to the specific papers for more detailed information regarding the sampling of fish and parasites.

Study design

The present thesis is empirical in its nature, using long-term observational data from a single study system. An obvious challenge to the analysis and interpretation of data from time series from a single system is the lack of a control lake. In an optimal world, the time series from the Takvatn system could be compared against time series from similar, unperturbed, nearby systems. This would allow us to separate climatological effects that act on a regional scale from local ecological changes within the lake. One must therefore approach the analyses and interpretation of data with care. In the present study, we have collected parasite infrapopulations from Arctic charr for more than three decades. My results are therefore limited to the infra- and component population levels. Processes operating on free-living stages and other host populations are unknown, although some of these can be inferred from ecological studies that have been conducted on these populations. Furthermore, any seasonal dynamics in parasite transmission are not dealt with here.

Previous studies on Arctic charr and its parasites from Takvatn

Takvatn has been extensively studied, both in terms of ecological interactions and host-parasite associations. In fact, previous studies have been conducted on all four parasite species investigated in the present thesis (Kristoffersen 1993; Amundsen et al. 1997; Knudsen et al. 2002; Henriksen et al. 2016). Rather than to repeat the analyses of these papers, I seek to build on the previous findings and put these host-parasite interactions into a longer time perspective. However, when defining my *a priori* hypotheses I have sought to seek support in general ecological theory rather than in system-specific knowledge. This is in line with the general recommendation of ecological analyses, which warns against testing hypotheses on the same data set used to generate those hypotheses (Tredennick et al. 2021). With this approach, I hope that the findings can be relevant to a broad readership.

Analyses

The goal of statistical analyses in ecology can broadly be divided into three categories; exploration, inference and prediction (Tredennick et al. 2021). Inference is the goal of the analyses in the present thesis, where the strength of explanatory variables is evaluated according to their ability to explain variation in the size of parasite infra- and component populations. The specific analyses used in the thesis are presented in the individual papers. Common to all three papers is the use of different regression analyses to infer relationships between the response and predictor variables. These methods are correlative, and care must be taken not to interpret spurious correlations as causative relationships. I have therefore been careful to clearly define my predictor variables *a priori*, based on ecological reasoning. Before a brief introduction to my main response and predictor variables, I would like to point to one predictor variable that was not included in any of the papers: Arctic charr diet. For the trophically transmitted parasite species addressed in **paper I** and **III**, feeding rates on copepods, sticklebacks (**paper I**) and *Gammarus lacustris* (**paper III**) determine parasite exposure. Unfortunately, the prime sampling for the long-term study programme in Takvatn is conducted in August each year. This corresponds to a period when the Arctic charr feed on superabundant insects that hatch during summer (Prati et al. 2021). Hence, the stomach contents from this period does not reflect the overall predation rates towards the intermediate hosts and were thus not included in my analyses.

Response variables

I have used different metrics to measure parasite population size over time. As mentioned in the introduction, parasite populations must be considered on several levels of organization. Here, I deal with infra- and component populations. For infrapopulations, I have used parasite abundance in individual fish as the response variable. Since these count data are overdispersed, they are analyzed with models that have negative binomial error structures. The most used metrics to describe component populations are prevalence, mean abundance and mean intensity (Bush et al. 1997). Mean abundance gives the average parasites number per host, and I have multiplied this measure with the density of Arctic charr to get an estimate of the total size of the component population. In addition, I wanted to see if the infection pressure (or force of infection) changed over time, and used logistic regression to calculate the age at 50 % probability of infection, a common approach in the modeling of diseases (McCallum et al. 2001; Heisey et al. 2006). For metazoan parasites, abundance-age could be a preferred option to prevalence-age curves as a measure of infection pressure. However, due to the aggregated distributions of parasites the abundance-age curves were associated with large uncertainty estimates that rendered comparisons across years inconclusive. An indirect approach was used in **paper III**, where random intercept and slopes were fit to the age-abundance relationship to test for differences among years in a mixed model. Furthermore, because of its management focus, **paper I** also included median intensity as a measure of parasite burden. This corresponds to the total number of parasites in the average fish in the infected part of the population, which was considered a more relevant assessment of the suitability of fish for recreational fisheries and consumption.

Predictor variables

The size and age of fish are predictor variables in all papers. For many organisms, obtaining accurate age estimates can be difficult and individuals are sometimes sorted into only two categories, juveniles and adults. For fishes at high latitudes, age is easy to estimate using the sagittal otoliths and counting the number of winter growth zones. This provides an easily obtainable and precise estimate of Arctic charr age (Baker and Timmons 2011). A more uncertain estimate I have used is catch-per unit effort (CPUE) as a proxy for host density (Harley et al. 2001; Maunder et al. 2006). Representing host populations as per unit area densities, rather than as actual counts, is recommended, as the relative proximity between hosts is more important for transmission than their total number (McCallum et al. 2001). To minimize the uncertainty surrounding this estimate, the measure is based on catches in August only to exclude any effects of month-to-month changes in fish activity, which could influence catchability. In addition, the same sampling method, multi-mesh gill nets, is used throughout the long-term studies at Takvatn. Furthermore, the CPUE estimates from Takvatn have proven adequate to estimate density-dependent food consumption rates in Arctic charr (Amundsen et al. 2007) and density-dependent interactions between Arctic charr and brown trout (Persson et al. 2007). Nonetheless, there might be small variation in CPUE due to for instance weather conditions that could generate or mask year-to-year fluctuations in density. As a measure of overall trends in the abundance of Arctic charr in the lake, however, the CPUE data is the best measure available and seemingly adequate. In **Paper II** I also expected a direct effect of temperature on the development of the parasite. However, indirect effects of temperature probably influence other aspects of Arctic charr ecology which in turn could influence parasite abundance. Modelling these interactions is complex and beyond the scope of this thesis, but references to such work are made where possible (e.g. Smalås et al. 2020).

Autocorrelation in the data

Time series vary in their degree of autocorrelation, measured as the autocorrelation function (ACF). The ACF is computed by calculating the correlation coefficient between pairs of values $L_{t-\tau}$ and L_t separated by lag τ ($\tau = 1, 2, 3,\ldots$), before these correlation coefficients are plotted as a function of lag τ (Turchin and Taylor 1992). The shape of the ACF provides insights into the stationarity and periodicity of population dynamics. Whereas stationary processes fluctuate around constant mean levels, nonstationary processes might suggest density independence, where regulation only occurs at extreme levels not encountered during the study (Turchin and Taylor 1992). Overall, the shape of the ACF provides information on long-term trends in the mean, cyclic patterns and stochasticity in population dynamics. For the most complete time series, *Salmincola edwardsii*, we present the ACF to provide insight into the population dynamics of this species (**paper 2**). This approach was avoided in the other two papers, as several years would have to be interpolated, and such interpolation is itself a generator of autocorrelation. Autocorrelation additionally poses some challenges when it comes to regression analyses. When autocorrelation was detected, I used generalized least squares that account for autocorrelation structures in residuals when analyzing temporal changes at the component population level.

The figures in this synopsis were made using www.BioRender.com

Summary of results

Summary of results from paper I

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

I studied the effects of fish culling on two *Dibothriocephalus* (Cestoda) species infecting Arctic charr in Takvatn, by monitoring infection levels prior to, during and in the decades following a mass removal of charr from the lake. These tapeworms use copepods as their first intermediate host, fish as second intermediate hosts and birds as final hosts (Figure 1c). 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. My two main research questions were, (a) did culling reduce the prevalence and intensity of *Dibothriocephalus* spp. in Arctic charr? and (b) are long-term trends in *Dibothriocephalus* spp. infections governed by Arctic charr density, demography or brown trout density?

The prevalence and intensity of *D. dendriticus* rapidly declined as Arctic charr density decreased. For *D. ditremus* there was no initial decline in prevalence and a slight increase in intensity a few years into the culling. However, infection levels decreased over the last 15 years of the study period. The lowest infections of both parasite species were observed during the last years of the study. Although there was a significant effect of Arctic charr density on *D. dendriticus*, the two most important predictors for both parasite species were host age and the density of brown trout.

The contrasting response of the two closely related species to culling was unexpected, and we discuss potential reasons for this disparity. Because the two species use the same intermediate host, reductions in copepod feeding could not explain the rapid decline of *D. dendriticus* compared to *D. ditremus*. Differences in spatial distributions of the two parasites in the lake (Kristoffersen 1993) coupled with shifts in the habitat utilization of Arctic charr following culling (Klemetsen et al. 1989, 2002) could potentially be one explanation for the observed discrepancies. Another explanation is reduced feeding on 3-spined sticklebacks (Prati et al. 2021), that are the main source of infection for this parasite in brown trout (Henriksen et al. 2016). The reductions in infection pressure may also suggest that transmission to birds was impaired for *D. dendriticus* but not for *D. ditremus*. As the two parasites use different bird species as hosts (gulls and ducks, respectively), differences in the response of the bird hosts to the fish removal is a potential explanation as well. Transmission of *D. ditremus* to birds have likely been maintained by the continued presence of sticklebacks with high infections of this parasite (Kuhn et al. 2015). However, since we do not have any infection data from birds or copepods it is difficult to pinpoint one exact mechanism for the observed patterns.

A clear result was that the shift in age structure from old to young fish reduced the component populations of both parasite species. A simple explanation for this is that younger fish have less time to accumulate high numbers of these parasites that survive and accumulate in the fish for years. Furthermore, as the brown trout population increased, the prevalence, intensity and infection rates of both parasites declined. Although large piscivorous brown trout become infected with both parasites, they are likely low-competent hosts for transmitting the parasites to birds. In this respect, piscivorous trout and piscivorous birds compete for the same prey items, small Arctic charr and 3-spined sticklebacks. The outcome of this competition is negative for these allogenic parasites that end up in a dead-end host rather than in their final host. The lowest infections of both parasites were observed 25 years after the culling was terminated. The increase in brown trout was a direct effect of the culling of Arctic charr, but took a decade post-culling to unfold and was mediated through size-structured competitive and predatory interactions between the two fish species (Persson et al. 2007, 2013). At the onset of the fish removal programme, a goal was to reduce infections of *Dibothriocephalus* spp. in Arctic charr. That this happened through brown trout diluting infections 20 years later was probably not the main hypothesis, but demonstrates how legacy effects following a large ecological perturbation can echo through a system for decades with consequences for multiple interacting species.

Main conclusions:

Culling overcrowded fish populations can reduce parasite transmission. However, the effects were mainly due to shifts in fish age structure and increased predation by brown trout. Accordingly, culling a population will affect multiple interacting species in the food web, which must be considered to understand and predict the effects on trophically transmitted parasites.

Summary of results from paper II

Long-term ectoparasite population dynamics driven by changes in host size but not host density or temperature

I studied the long-term dynamics of infection with a directly transmitted copepod parasite, *Salmincola edwardsii* (gill lice), in Arctic charr (Figure 1a). This parasite infects the gills of Arctic charr where it can cause respiratory problems (Sutherland and Wittrock 1985; Mitro 2016). However, whereas prevalence and intensity can be high in lotic environments (Mitro 2016), infections in lakes are typically low and probably not subject to density-dependent regulation (Amundsen et al. 1997). Previous studies suggest that host size is a key metric for transmission of parasites that are contact-transmitted, such as gill lice (Poulin et al. 1991; Grutter and Poulin 1998). I thus expected host size to be the most important predictor of infrapopulation size, and that shifts in the size-structure of the host population would affect component population size. Since this parasite has a direct life cycle with a free-living infective copepod stage, transmission should depend more on host density than trophically transmitted parasites do. An analogous and comparable host-parasite system is the well-studied association between sea lice and salmonids in the ocean. Here, large host densities in fish farms amplify transmission to wild salmonids (Krkošek et al. 2005; Sandvik et al. 2016). However, at natural host densities, Allee effects in the parasite population reduce mating probabilities which limits the population growth of sea lice (Krkošek et al. 2012; Cox et al. 2017). I therefore also explored the extent to which host density directly affected parasite transmission rates. Furthermore, as brown trout is not a host for this parasite, we expected increasing trout densities to dilute transmission of *S. edwardsii* to charr. Finally, development of the parasite is temperature dependent (Johnston and Dykeman 1987; Poulin et al. 1990; Vigil et al. 2016), and I examined the effects of temperature on the long-term dynamics of the parasite.

As hypothesized, I found that infrapopulations increased with fish size, and that component population size and growth were highly dependent on changes in the size-structure of the fish population. I did not detect any effects of host density on parasite transmission rates. Contradictory to our hypothesis, there was a slightly positive effect of brown trout density on infections in charr. A potential mechanism for this surprising result is related to the observation that Arctic charr in the profundal zone tended to have higher infections of *S. edwardsii*, and that more Arctic charr resided in the profundal areas in years with higher densities of brown trout in the littoral, thereby increasing parasite exposure. Finally, there were no direct effects of temperature on gill lice infections.

Main conclusions

Changes in the size-structure of the host population explained much of the variation in the population dynamics of *S. edwardsii*. The autocorrelation functions of the host and parasite populations displayed different temporal dynamics, suggesting that the parasite population does not track changes in the density of its host. Infrapopulations typically consisted of one or a few parasite individuals, which might impose mating limitations and induce Allee effects on parasite population growth. Since Arctic charr body size is negatively correlated with fish density, there might exist a counter-intuitive negative association between fish density and parasite population size. For contact-transmitted parasites in open lake systems, fewer and larger hosts might be preferable to more numerous but small-sized hosts.

Summary of results from paper III

Fish age and population size structure affect the abundance and aggregation of a long-lived nematode parasite

In **paper III** I analyzed infections of the swimbladder nematode *Cystidicola farionis* in Arctic charr. The parasite uses the amphipod *Gammarus lacustris* as its only intermediate host and Arctic charr as its only final host (Figure 1b), and can survive in the swimbladder of charr for > 10 years. The main goal was to evaluate potential long-term drivers of parasite abundance and aggregation. Specifically, we were interested in the distribution of the parasites among age classes, and the interrelationships between temporal changes in host age, parasite abundance and parasite aggregation. We additionally investigated how heterogeneity in Arctic charr feeding mode (benthic versus pelagic) and body size influenced parasite aggregation. To measure aggregation, we used two recently proposed methods. The Hoover index, similar to the Gini coefficient or Poulin's *D*, simply measures departure from a uniform distribution (McVinish and Lester 2020). The second method uses feasible set theory to measure aggregation beyond the constraints imposed by the number of parasites and hosts in the sample (Johnson and Wilber 2017). We used structural equation modeling to infer direct and indirect causal relationships between host age, size, feeding mode, and parasite abundance and aggregation. It was difficult to separate host age and size as predictor variables, as the two were highly correlated. We chose to focus on host age, since old fish, in addition to being of a large size, have had more years to accumulate nematodes in the swimbladder.

We found that host age was positively associated with *C. farionis* abundance, which in turn negatively affected parasite aggregation. The relationship between host age and parasite aggregation was thus negative, and remained stable over the study period. The collection of swimbladder nematodes began after the initiation of the culling experiment and we could therefore not directly address the effects of the culling effort on parasite abundance. However, fish born earlier than 1986 had lower infections of *C. farionis,* suggesting that the increased consumption rates and habitat and dietary shifts following culling positively affected *C. farionis* transmission to Arctic charr. Heterogeneity in size and feeding mode positively affected aggregation as hypothesized, but these effects were much less clear when the data were divided into age classes.

Main conclusions

Our predictor variables failed to account for more than half the variation in parasite aggregation. This supports the stochastic and dynamic nature of parasite aggregation observed elsewhere. That being said, we found clear evidence that temporal variation in parasite abundance and prevalence set the boundaries for aggregation, and that temporal changes in parasite abundance were governed by the age and size structure of the host population. The abundance and prevalence were high and fairly stable throughout the study period, particularly when the oldest cohorts were omitted from the analysis. This could suggest that regulatory factors are operating, but probably relates more to stability in the feeding ecology of Arctic charr during the past few decades in Takvatn.

Discussion

In this thesis I provide novel information on the long-term dynamics of infection with metazoan parasites in a size- and age-structured fish population. My results shed light on how changes in the free-living community affect host ecology, which in turn shape long-term patterns in parasite population dynamics. Combining the findings from the present thesis with long-term studies on the ecology of Arctic charr from Takvatn allows us to make some general predictions as to how host density, feeding and body size interact to shape long-term parasite transmission dynamics (Figs 1 and 2). These findings should be valuable for ecological research and fish population management and can stimulate avenues for further research efforts.

The effect of Arctic charr density on parasite transmission

There were no clear direct effects of host density on the temporal dynamics of parasite infection (**papers I and II**). This does not mean that the density of Arctic charr has not affected parasite transmission in the system. Long-term studies from Takvatn show that the density of Arctic charr affects several aspects of its ecology. In particular, the interplay between fish density, food consumption and body size is important for parasite transmission (Figure 2). In the epidemiological literature, transmission is considered as the rate at which susceptible hosts are converted into infected individuals (Begon et al. 2002). This transmission rate is proportional to the contact rate between susceptible hosts and parasite infective stages. For microparasites, and for macroparasites with direct life cycles, this contact (and transmission) rate increases with density of susceptible hosts (Anderson and May 1979; May and Anderson 1979). In light of this, the lack of an effect of Arctic charr density on *Salmincola edwardsii* transmission was surprising. However, when considering the importance of host size for *S. edwardsii* transmission (**paper II**) and the negative relationship between Arctic charr density and body size (Figure 3c), that result was not as surprising. For hosts with indeterminate growth, trade-offs between host body size and host density should therefore be considered when modelling transmission dynamics.

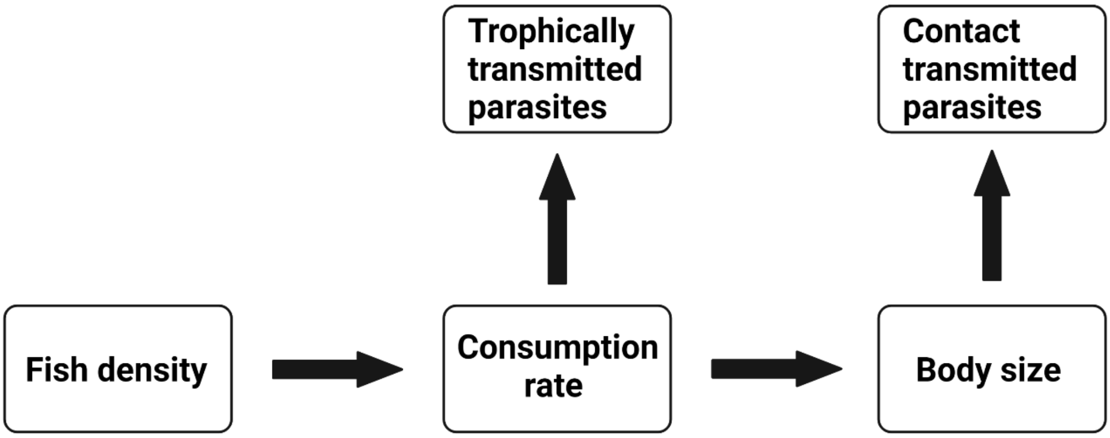

Figure 2. Conceptual diagram showing the causal relationships (arrows) between fish density, consumption rate and body size, and their effects on the transmission of trophically transmitted parasites versus parasites that are transmitted through contact with infective stages in the environment.

For trophically transmitted parasites, transmission rates depend on the consumption rates of downstream hosts (predators) towards intermediate hosts (prey). For Arctic charr there is a strong inverse relationship between consumption rates and fish density, a relationship likely to be observed in other fish species as well (Figure 3a, Amundsen et al. 2007). This negative association is mediated by competition for limited resources, and constitutes the mechanism for the negative association between fish density and body size (Figure 3a-c). Increased consumption rates increase fish size and transmission of trophically transmitted parasites

(Figures 2 and 3b). However, most fishes have size-dependent ontogenetic dietary shifts (Sánchez-Hernández et al. 2019). For such populations, shifts in the size structure alter the exposure to parasites with different intermediate hosts. The main effect of Arctic charr density on parasite transmission is likely through density effects on feeding rates and body size that in turn determine parasite exposure (Figure 2), and the nature of size-structured interactions in the fish population is thus key for understanding parasite transmission.

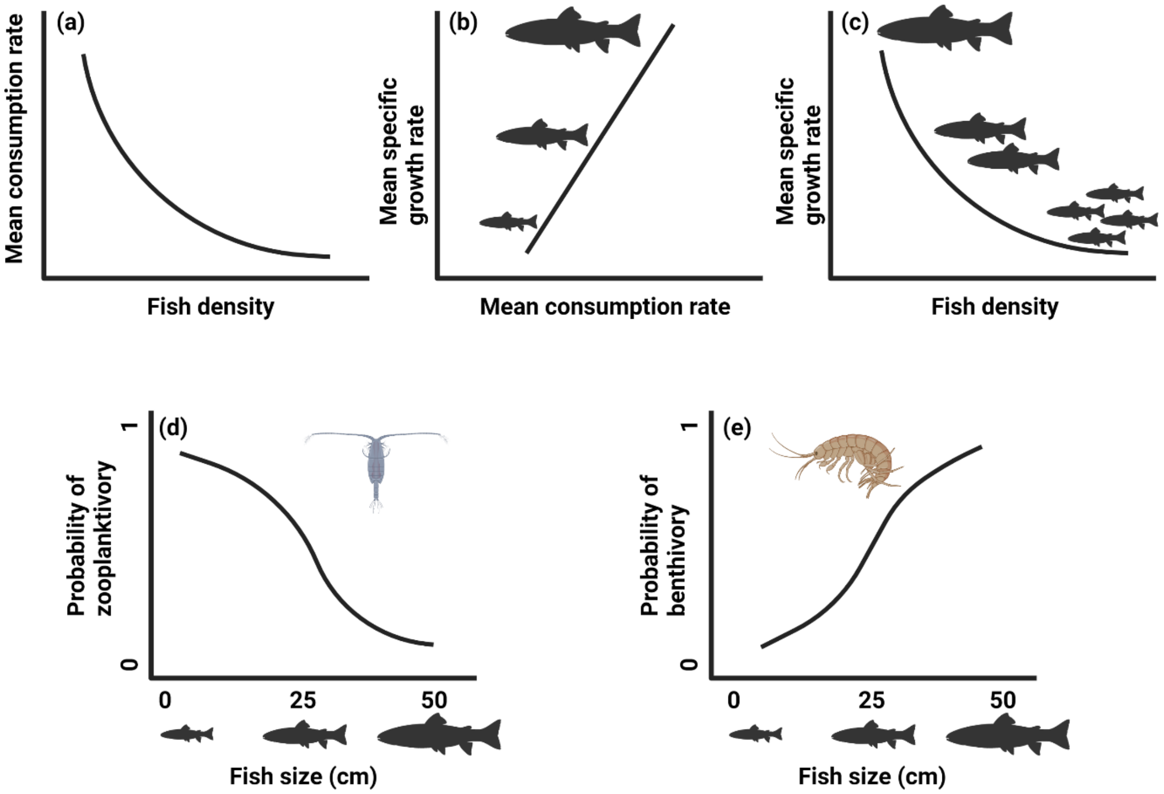

Figure 3. Figures a – c shows the association between fish density, consumption rates and mean specific growth rate for Arctic charr in Takvatn. Figures d and e show the probability of Takvatn charr consuming zooplankton (d) and benthos (e) with increasing fish size. The figures are based on the findings of Amundsen et al. (2007, unpublished data).

Parasitism in age- and size-structured host populations

The age and size-structure of the fish population were the most important structuring mechanisms for all four parasite species. Given the numerous studies from fishes describing the relationship between host age, size and parasite infection this was hardly a surprising result (Zelmer and Arai 1998; Lo et al. 1998; Poulin 2000). In fact, Dogiel (1961) already pointed to the importance of host age and food consumption for trophically transmitted parasites, and body surface area available for the attachment of ectoparasites. However, a novel aspect in this regard is the present highlighting of how dynamic these properties of the host can be, and the implication this has for long-term variation in parasite populations. Another important finding was how competitive and predatory interactions in the free-living community directly and indirectly shape parasite infections over time. Competitive and predatory interactions among fishes are considered to be size-structured (Post et al. 1999; de Roos and Persson 2013). Changes in the size-distribution of the host thus affects size-structured interactions between the host and its predators and prey, with important implications for parasite transmission. So how did fish size and age affect the long-term dynamics of the metazoan parasites addressed in the present study?

Many helminths are long-lived and older hosts accumulate parasites over time (Dogiel 1961; Hemmingsen et al. 2000). **Papers I** and **III** highlight the importance of host age structure in regulating the abundance and distribution of helminth parasites. Although many host-parasite models consider the age distribution of the host population as a fixed constant through time, some have investigated the importance of temporal shifts in host demography for parasite transmission. In Atlantic cod (*Gadus morhua*) for instance, yearly differences in growth rate combined with shifts in the age and size distribution of fish, explain inter-annual variation in sealworm (*Pseudoterranova decipiens*) burden (Des Clers 1991). In this host-parasite system where cod is the second intermediate host, fishing-induced shifts towards a younger age structure reduced infection levels in fish despite increases in the final host population of seals (Des Clers and Wootten 1990). These findings harmonize with our results in **paper I**, where culling-induced shifts in the age structure of the host reduced the abundance of *Dibothriocephalus* parasites. In both of these systems, considering the abundance of final hosts (birds and seals) was not necessary to account for parasite infections in fish. Although final host density has explained the abundance of parasites in intermediate hosts elsewhere (Hechinger and Lafferty 2005), the findings from cod and Arctic charr suggests that for parasites that use fish as intermediate hosts, the density of the final hosts is not the main driver of parasite abundance.

Although culling reduced the age of Arctic charr, it simultaneously facilitated an increase in consumption rates and body size through release from intraspecific competition (Amundsen et al. 2007). As mentioned earlier, cumulative increases in feeding facilitates exposure to trophically transmitted parasites (Figure 2). However, while increasing consumption rates towards one prey taxon increases exposure to parasites transmitted from that specific prey, a change in the utilized prey taxa may shift the exposure from one set of parasites to another. The culling induced changes in fish size that altered the ontogenetic dietary shifts (Prati et al. 2021), which apparently both reduced (**paper I**) and increased (**paper III**) parasite transmission to Arctic charr, depending on the specific parasite and intermediate hosts involved. Understanding the nature of ontogenetic dietary shifts is therefore crucial to predict how shifts in host size distribution will affect parasite transmission. As organisms grow, they may switch their prey types to meet enhanced energetic demands. In fishes, prey size increases with fish body size due to differences in handling capabilities with increasing body (and thus mouth gape) size (Sánchez-Hernández et al. 2019). This leads to ontogenetic dietary shifts, typically from zooplankton at small sizes, to zoobenthos and fish at large fish sizes (Sánchez-Hernández et al. 2019). For Takvatn charr the size at which fish shift from zooplankton to benthos feeding occurs around 25 cm (Figures 3d and e). Pre-culling, there were hardly any fish above this size (Klemetsen et al. 2002), whereas the post-culling temporal changes in fish size distributions shifted the population from being dominated by a zooplanktivorous ontogenetic stage to a benthivorous stage, resulting in a radical shift in the exposure to trophically transmitted parasites. Although **paper II** highlights the importance of temporal changes in fish size for contact-transmitted parasites, it is unfortunate that we do not have information regarding the infection levels of gill lice when the fish population was dense and consisted of small-sized individuals.

The role of brown trout in mediating parasite transmission to Arctic charr

The competence and competitive ability of alternative hosts shape disease transmission in focal hosts (Cortez and Duffy 2021). From the present long-term studies of fish parasites in Takvatn, another fish species emerged as important for parasite transmission to Arctic charr, namely brown trout. Increases in the densities of this competitor and predator diluted (**paper I**) and facilitated (**paper II**) parasite transmission to Arctic charr. In **paper I,** brown trout likely removed *Dibothriocephalus* parasites from the lake by feeding on intermediate hosts whilst simultaneously being a low-competence host for onward transmission (Barron et al. 2015). In **paper II**, the presence of brown trout forced Arctic charr to congregate in deeper waters that facilitated exposure to *Salmincola edwardsii*. For Arctic charr, the use of profundal areas probably reduces interspecific competition and predation risk for smaller individuals. The escape from predation by brown trout in the littoral zone facilitated parasite transmission in the profundal for smaller Arctic charr individuals. This illustrates the trade-off between predator-induced fear effects and parasite avoidance behaviours (Behringer et al. 2018). In this case, fear of predation outweighed risk of parasitism, which is to be expected given that predation effects are lethal whereas parasitism usually is not (Doherty and Ruehle 2020; Daversa et al. 2021).

Besides being a low competence host for *Dibothriocephalus* and altering Arctic charr habitat use and exposure to *Salmincola*, brown trout probably affects parasite transmission in several ways. An indirect effect of brown trout on parasite transmission to Arctic charr not explicitly considered in the present thesis, is the role of predatory brown trout in regulating Arctic charr population abundance (Persson et al. 2007). This will influence consumption rates and body size of charr, thereby affecting parasite transmission rates (Figures 2 and 3). Furthermore, interspecific competition with brown trout shapes dietary niche widths and prey choice of Arctic charr, which should alter their exposure to trophically transmitted parasites (Nilsson 1963; Prati et al. 2021). This illustrates the importance of considering interactions such as competition and predation in the free-living community when seeking to explain parasite abundance and transmission in natural environments.

My findings on the effects of brown trout on parasite transmission to Arctic charr adds to the knowledge on how competence, competitive ability and predatory ability of alternative species shape parasite transmission to hosts (Ostfeld and Keesing 2012; Baudrot et al. 2016; Strauss et al. 2018). Such effects should be considered in other aquatic ecosystems, for instance when considering the effects of changing fish distributions on parasite transmission. The increase in relative abundance of brown trout compared to Arctic charr is observed in other northern freshwater ecosystems as well, due to climate change and increasing water temperatures (Finstad et al. 2011; Svenning et al. 2021). This follows a general trend, where warm- and cool-water freshwater fishes are expanding their ranges, facilitating increased overlap with cold-water species like Arctic charr (Comte et al. 2013; Rolls et al. 2017). Invasive species can co-introduce parasites (spillover effect), function as alternative hosts for native parasites (spillback effect) or function as sinks for native parasites (dilution effect), depending on their competence as hosts (Kelly et al. 2009; Goedknegt et al. 2016). However, apart from understanding the competence of these new hosts as reservoirs for parasites, the findings of the present study emphasize that it is important to account for their effect on the ecology of native fish species to understand how they will affect parasite transmission in recipient ecosystems.

Stability and regulation of parasites and hosts

Paper III was the only paper to address potential regulation of the parasite population. As infection pressures rose with size and age, aggregation declined, thereby indicating a possible ceiling for infrapopulation size. The mechanism could be due to mortality of hosts or parasites, or simply lack of space in the swimbladder for the establishment of new parasite individuals. Whatever the mechanism, the results show that infrapopulations, and thus the component population, are regulated through density dependent processes. I refrained from using aggregation to infer regulation of *Dibothriocephalus* spp. and *Salmincola* due to their low abundances. As mean abundance approaches zero, aggregation estimates become increasingly inflated, and it becomes difficult to distinguish biological phenomena from statistical artifacts (Wilber et al. 2017; McVinish and Lester 2020). Kristoffersen (1993) performed an in-depth analysis on the *Dibothropcephalus* spp. material from 1980-81 included in the present thesis. Age-specific mean abundance and variance to mean ratios suggested mortality of hosts heavily infected with both *Dibothriocephalus* species. The method used to infer mortality by Kristoffersen (Anderson and Gordon 1982) cannot rule out other regulatory mechanisms which may have generated the observed patterns (Pacala and Dobson 1988; Wilber et al. 2016). Nevertheless, the potential pre-culling density-dependent regulation of *Dibothriocephalus* populations is likely not operating following the increase in fish size (increasing host tolerance) and reductions in parasite abundance (reducing pathogenicity) observed from 1987 and later (**paper I**). This might suggest decreased regulation of *Dibothriocephalus* over time and increased regulation of *Cystidicola* due to an inverse relationship in the abundance of the two species (**paper III**). For the gill lice, the prevalence and abundance of *Salmincola* in Takvatn is low compared to other systems, suggesting that density-dependence is not constraining parasite population size (Mitro and Griffin 2018; Boone and Quinlan 2019). More plausible, the low prevalence and abundance might limit *Salmincola* population growth through Allee effects (**paper II**).

Throughout the thesis, I have explained how host attributes affect various measures of parasite population size and growth. However, I have not asked how parasites might affect host abundance and ecology. This might seem odd, considering the vast amount of literature showing that parasites affects numerous aspects of the host that could influence parasite transmission directly or indirectly. For instance, parasites can regulate host abundance (Hudson et al. 1998) and affect interspecific competition and predation between hosts (Hatcher et al.

2006, 2014). In zooplankton, parasites destabilize host populations by shifting stage-structured interactions (Hite et al. 2016). Similar mechanisms could potentially affect the structure and ecology of fish populations. Arctic charr is host to several metazoan parasite species, including at least eight different genera with > 10 species in Takvatn (Amundsen et al. 2009; Kuhn et al. 2016; Soldánová et al. 2017). These inhabit diverse organs as the gills, eye, swimbladder, body cavity, gall bladder and intestine. Each of these species could potentially regulate host abundance and ecology, with potentially synergistic effects from multiple species (Rynkiewicz et al. 2015). Detecting such effects was beyond the scope of this thesis. Furthermore, interspecific interactions with brown trout is convincingly shown to be the main determinant of Arctic charr abundance and size-structure (Persson et al. 2007, 2013). Thus, if parasitism affects the ecology of Arctic charr in Takvatn, the effects were likely more pronounced prior to the comeback of brown trout in the system.

Conclusion and future perspectives

The present thesis highlights the importance of considering different ecological interactions for understanding long-term trends in parasite abundance in fishes. A future goal should be to use these data to predict how for instance changes in temperature and fishing pressure (Smalås et al. 2020) may affect parasite transmission in aquatic ecosystems. To realistically model parasite transmission to fish, competitive and predatory interactions among hosts, and between hosts and non-hosts, should be included. Such efforts may seem overwhelming. A starting point might be to integrate the field of size-structured population modeling with parasite population models. Size-structured population models have made it possible to connect size-dependent individual processes and their effects on population and community dynamics which in turn feedback on body-size distributions (Persson and de Roos 2003, 2007). These models provide information on the abundance and size distribution of fish species. With information on size-dependent transmission rates obtained from long-term data, it is possible to subsequently model parasite abundance per fish. This could thus allow us to predict the size of both infra- and component populations of parasites.

Long-term studies in ecology have provided key insights into processes that drive population and community dynamics (Franklin 1989). In this thesis, I was able to unravel some important pathways that structure the long-term dynamics of fish parasites. Some of the ecological processes involved took a long time to unfold, and I would not have detected their role in shaping parasite population dynamics in a short-term study. My findings highlight how managing fish populations have direct and indirect effects on parasite populations, and the ecological phenomena involved. I hope that this helps stimulate further research and provide incentives to establish and continue similar long-term research programmes elsewhere.

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Paper I

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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 can indirectly reduce 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
Dibothriocephalus, *Diphyllobothrium*, fish parasites, fishing, host culling, host–parasite interactions, long-term study, whole-lake experiment

1 | 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 et al., 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 a 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, Sandin, Zgliczynski, Guerra, & Micheli, 2014; Wood et al., 2010). 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. Cardon, Loot, Grenouillet, & Blanchet, 2011; Zelmer & Arai, 1998) 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., 2019).

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 et al., 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 (*Salmo trutta*) 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., 2019; 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, (a) did culling reduce *Dibothriocephalus* spp. prevalence and intensity in Arctic charr? and (b) 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 does *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).

2 | MATERIALS AND METHODS

2.1 | 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 phosphorus levels not exceeding

5 μg/L (Eloranta, Knudsen, & Amundsen, 2013). The lake has three fish species; brown trout, 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, 2019; Klemetsen et al., 2002). This resulted in a new stable state with coexisting large charr and trout (Amundsen et al., 2019; Klemetsen et al., 2002; Persson et al., 2007).

2.2 | Sampling

Charr individuals analyzed in this 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 hr 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 (g), measured in fork length (mm), and sex and gonad maturation were recorded. Otoliths were used for age determination. Charr and trout densities were measured as CPUE (fish caught per 100 m^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).

2.3 | Parasite life cycles

The two cestodes *D. 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.

2.4 | 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 generalized least squares (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 regression coefficients to a variable and estimates the time point when coefficients change, that is, there are two different linear trends on each side of the breakpoint. The slope and confidence intervals (CI) for the two linear trends are provided, as well as the R^2 value for their combined fit.

Infections in the charr population could change because of other ecological factors than altered parasite abundance in the ecosystem, for instance through truncated age structure or diet shifts in older charr. If so, the *Dibothriocephalus* spp. infection pressure on young charr, the ontogenetic stage where charr feeds most on zooplankton (Amundsen, Knudsen, & Klemetsen, 2008), should remain constant. We used logistic regression to analyze if the relationship between infection and charr age changed before, during, and over four 5-year periods after culling. Infection was the binomial response variable and charr age the predictor. From these models, we calculated the age at which there was a 50% probability of charr being infected with *Dibothriocephalus* spp. Models for individual years showed a similar pattern as the overall periods, and results from these are provided in the supplementary material (Tables S4 and S5).

To track relative changes in the parasite component population ("ecological abundance" sensu Wood et al., 2013) of the two *Dibothriocephalus* species in charr, we multiplied the mean abundance of the respective parasite species per charr by charr density (CPUE) within each year.

Finally, we tested associations between *Dibothriocephalus* spp. intensity and prevalence, and predictor variables (charr age, length, density and trout density) with GLS models fit using GLS from the R package NLME (Pinheiro, Bates, DebRoy, & Sarkar, 2018). In all models, we 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 versus 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 modeling (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.

3 | RESULTS

3.1 | 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 (Figures 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 (Figures 1 and 2). The variation in intensities decreased throughout the study period (Figures 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 (Figures 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*.

3.1.1 | Infection rate

Dibothriocephalus dendriticus infection rates declined after culling (Figure 3). The age at which half the charr were infected also increased throughout the study period (Figure 3). Before the fish removal, half the charr were infected by 2- (95% CI 1.6–2.6) years (Figure 3). By 1987–1988, half the charr were infected by 5.7 (4.9–6.6) years

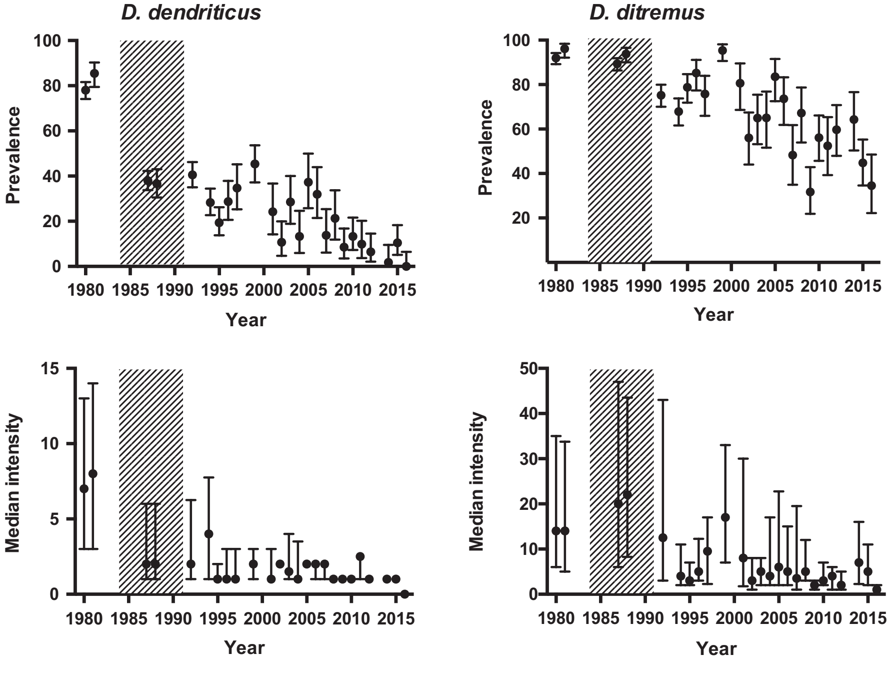

FIGURE 1 Prevalence (top, with 95% confidence intervals) and median intensity (bottom, with 25 and 75 percentiles) for *Dibothriocephalus dendriticus* (left) and *Dibothriocephalus ditremus* (right) in Takvatn in years sampled. The hatched area indicates the culling period

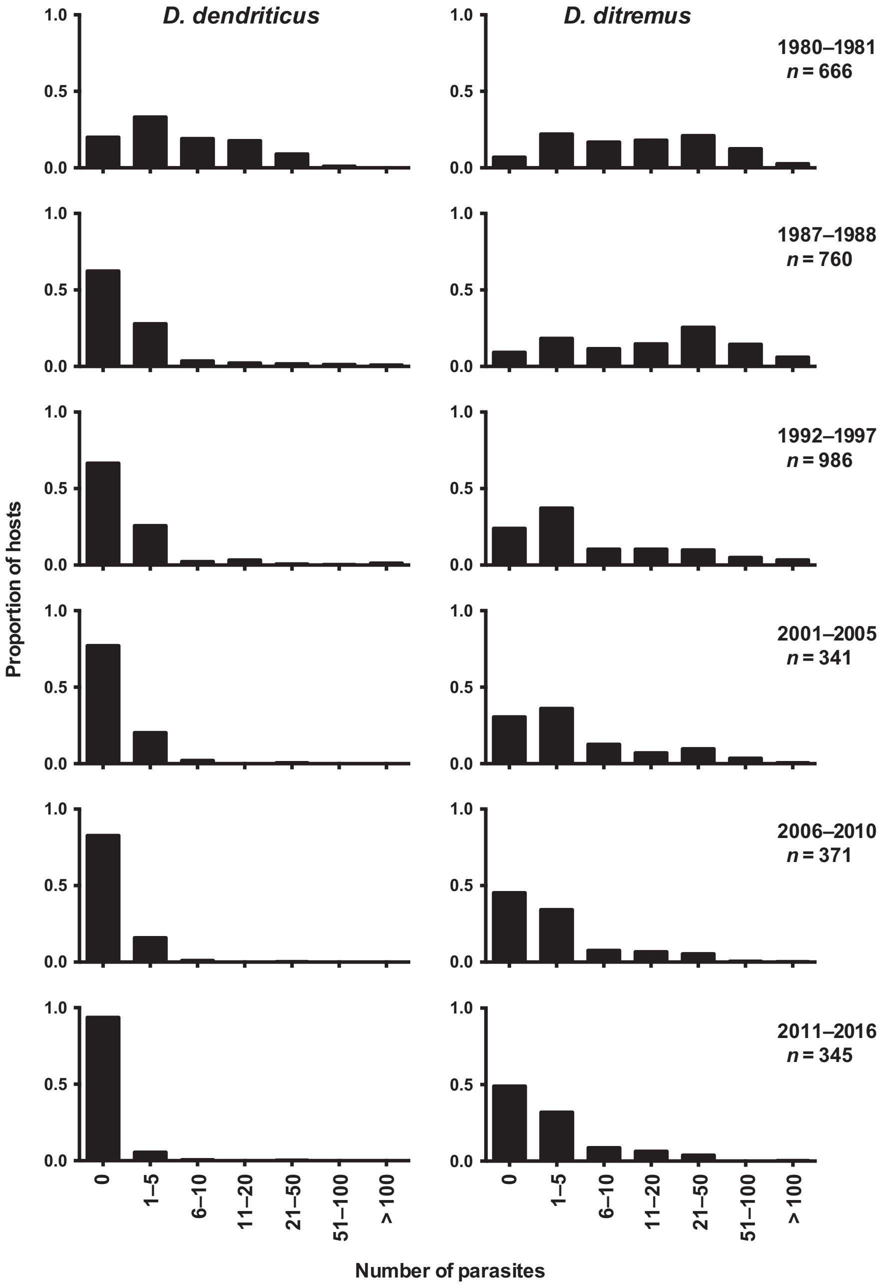

FIGURE 2 Proportional distributions of Arctic charr with different abundances of *Dibothriocephalus dendriticus* (left) and *Dibothriocephalus ditremus* (right) for six different time periods in Takvatn

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 (Figure 3). Before the fish culling, half the charr were infected by 2.6 (2.2–3.2) years (Figure 3). This decreased to 1.9 (1.7–2.3) years in 1987–1988. By 2001–2005 half the charr were infected by 3.1 (2.7–3.6) years, whereas at the study's end, half the charr were infected by 4.3 (3.3–5.3) years.

3.1.2 | Parasite population size

The tapeworm component population (i.e., total tapeworms in the charr population rather than per fish) in Arctic charr declined exponentially after culling (Figure 4). In the last ~10 years of the study, the *D. ditremus* population had declined 7–10-fold and the *D. dendriticus* population declined 20–60-fold compared to pre-culling years (Figure 4).

3.2 | Are long-term trends in prevalence and intensity governed by charr density, demography or brown trout density?

The effect of the predictors *charr age*, *charr length*, *charr density*, and *trout density* on parasite prevalence and intensity differed between the two parasite species (Table S3). For *D. dendriticus*, prevalence was positively associated with charr age ($F_{1,33}$ = 24.0, p < 0.001, slope = 8.05 ± 1.64 SE) and charr density ($F_{1,33}$ = 10.4, p = 0.003, slope = 0.65 ± 0.20), but negatively associated with trout density ($F_{1,33}$ = 38.7, p < 0.001, slope = −17.30 ± 2.78)

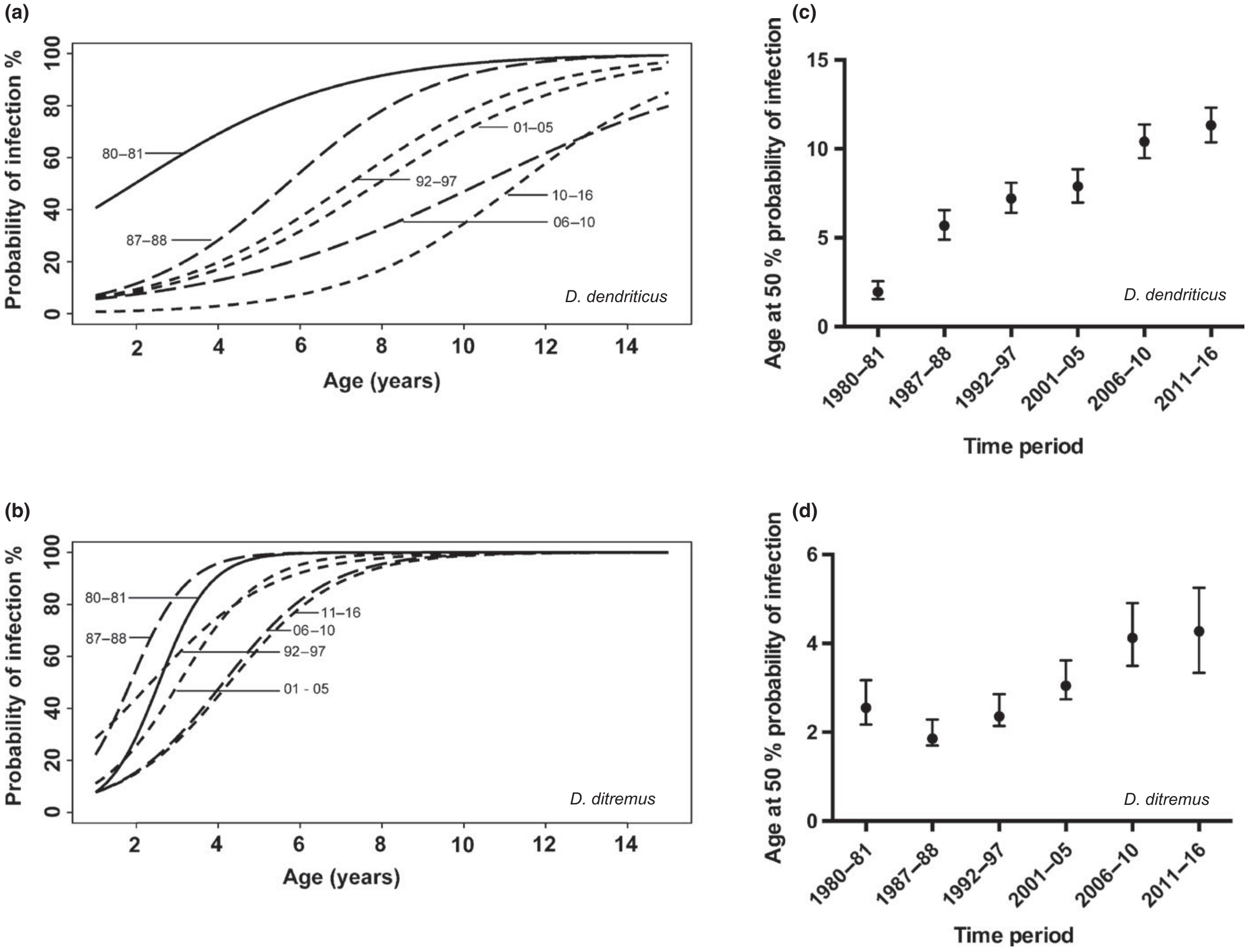

FIGURE 3 Logistic regression showing the probability of infection with increasing charr age for *Dibothriocephalus dendriticus* (a) and *Dibothriocephalus ditremus* (b) during six different time periods in Takvatn between 1980 and 2016. The two graphs on the right side show the age (±95% CI) at which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

(model $r^2 = 0.86$; Table S3). Similarly, *D. dendriticus* intensity was positively associated with charr age ($F_{1,33} = 44.7$, $p < 0.001$, slope = 1.39 ± 0.21) and charr density ($F_{1,33} = 23.9$, $p < 0.001$, slope = 0.11 ± 0.02), but was negatively associated with charr length ($F_{1,33} = 30.1$, $p < 0.001$, slope = −0.04 ± 0.01) (full model $r^2 = 0.86$; Table S3). For *D. ditremus*, neither prevalence nor intensity were associated with charr density. *Dibothriocephalus ditremus* prevalence was negatively associated with trout density ($F_{1,34} = 111.4$, $p < 0.001$, slope = −23.11 ± 2.19) and positively associated with charr length ($F_{1,34} = 27.7$, $p < 0.001$, slope = 0.32 ± 0.06) (model $r^2 = 0.77$; Table S3). The splined data for *D. ditremus* intensity created a bell-shaped curve from 1980–1981 to 1987–1988 that prevented the autocorrelation structure from being correctly modeled, 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 $r^2 = 0.69$).

4 | 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

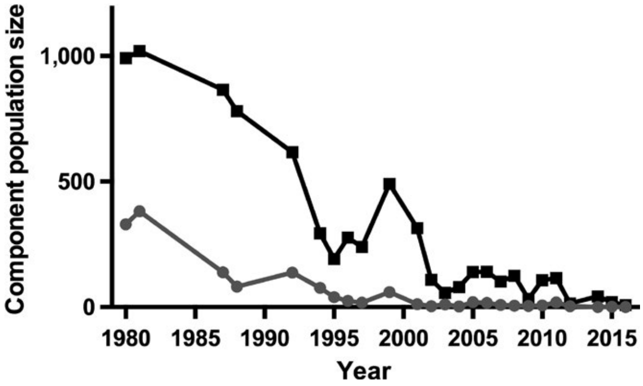

FIGURE 4 Estimated component population size of *Dibothriocephalus dendriticus* (grey lines, circles) and *D. ditremus* (black lines, squares) in Arctic charr from Takvatn

(Halvorsen & Andersen, 1984; Henricson, 1977; Henriksen et al., 2016). When culling increases host mortality, age distributions can favor younger fish, as seen for fisheries (Berkeley, Hixon, Larson, & Love, 2004), resulting in fewer accumulated parasites. This appears to be the case in this 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 & Knudsen, 2013; Klemetsen et al., 2002) 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 young and small charr from the profundal and pelagic to the littoral (Klemetsen, Muladal, & Amundsen, 1992; Klemetsen et al., 2002). 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, Amundsen, Nilsen, Kristoffersen, & Klemetsen, 2008; Knudsen, Curtis, & Kristoffersen, 2004) as seen for European whitefish (*C. 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, Amundsen, & Klemetsen, 2002; Knudsen, Kristoffersen, & Amundsen, 1999). 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, 2019). 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.

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AUTHORS' CONTRIBUTIONS

E.H.H., A.M.K., K.D.L., P.-A.A., Ro.K. and Ru.K conceived the ideas and designed methodology; E.H.H., P.-A.A., Ro.K. and Ru.K. collected the data; E.H.H. and A.F. analyzed the data; E.H.H. led the writing of the manuscript with additional contributions from A.F., K.D.L and P.-A.A. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Supporting information to

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Table S1. Summary statistics of charr sampled for the present study. Number of charr (N) and their mean age (years) and length (mm). CPUE (catch per unit effort) of charr and trout in Takvatn. P = prevalence, MA = mean abundance, MI = median intensity, Var/mean = variance of abundance divided by mean abundance for *Dibothriocephalus dendriticus* and *D. ditremus*.

Year	N	Age	Length	CPUE charr	CPUE trout	P	MA	MI	Var/mean	P	MA	MI	Var/mean
						Dibothriocephalus dendriticus				***Dibothriocephalus ditremus***			
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**

Table S2. Results from breakpoint analyses 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)

Table S3. Results from GLS models predicting *Dibothriocephalus dendriticus* and *D. ditremus* prevalence and intensity after AIC model selection. Autoregressive (AR) or moving average (MA) correlation fitted to models where needed.

Response variable	**Model summary**	**Predictor**	**Coef ± s.e.**	**F-value**	**P-value**
Dibothriocephalus dendriticus prevalence	full model $r^2 = 0.86$, Correlation structure: AR MA (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: AR MA (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: AR MA (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
Dibothriocephalus ditremus intensity (log)	full model $r^2 = 0.69$, Correlation structure: AR MA (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

Table S4. Summary of the logistic regression models of *Dibothriocephalus dendriticus* probability of infection predicted by 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				

Table S5. Summary of the logistic regression models of *Dibothriocephalus ditremus* probability of infection predicted by 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	-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				

Paper II

Henriksen, E.H., Frainer, A., Poulin, R., Knudsen, R. & Amundsen, P.A.

Long-term ectoparasite population dynamics driven by changes in host size but not host density or temperature.

Manuscript.

Long-term ectoparasite population dynamics driven by changes in host size but not host density or temperature

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Author contribution statement

All authors conceived ideas and developed methodology. EHH, RK and PAA conducted fieldwork. EHH and AF analysed the data. EHH led the writing of the manuscript with contributions from AF and RP. All authors contributed critically to the drafts and gave final approval for publication.

Abstract

Host density, host body size, and ambient temperature have all been associated with increases in parasite infection. However, the relative importance of these factors in shaping long-term parasite population dynamics in wild host populations is unknown due to the absence of long-term studies. Here, we examine long-term drivers of gill lice (Copepoda) infections in Arctic charr (Salmonidae) over 32 years. We predicted that host density and body size and water temperature would all positively affect parasite population size and population growth rate. Our results show that fish size was the main driver of gill lice infections in Arctic charr. In addition, Arctic charr became infected at smaller sizes and with more parasites in years of higher brown trout population size. This is explained by negative intraguild interactions between brown trout and Arctic charr, which drive smaller Arctic charr to seek refuge in deeper areas of the lake, increasing infection risk. There was no effect of host density on the force of infection, and the relationship between Arctic charr density and parasite mean abundance was negative, possibly due to an encounter-dilution effect. The population densities of host and parasite fluctuated independently of one another. Water temperature had negligible effects on the temporal dynamics of the gill lice population. Understanding long-term drivers of parasite population dynamics is key for researchers, managers, and practitioners. In fish farms, artificially high densities of hosts lead to vast increases in the transmission of parasitic copepods. However, in wild fish populations fluctuating at natural densities, the surface area available for copepodid attachment might be more important than the density of available hosts.

Key-words: host density, gill lice, *Salmincola edwardsii*, Arctic charr, *Salvelinus alpinus*

Introduction

A central assumption to most host-parasite models is that parasite transmission increases with host density (May and Anderson 1979; Hopkins et al. 2020). Spatial studies and meta-analyses support this association for directly transmitted parasites. For instance, the density of parasitic snails is positively associated with the density of their sea urchin host (Sonnenholzner et al. 2011), and the prevalence and abundance of directly transmitted nematodes increase with host density in mammals (Arneberg et al. 1998; Arneberg 2001; Stringer and Linklater 2015). In freshwater ecosystems, dense and stable host populations also have dense and stable populations of directly transmitted parasites, even though infection risk per host can decrease with increasing host density due to encounter-dilution effects (Lagrue and Poulin 2015; Buck and Lutterschmidt 2017). Altogether, host density should regulate populations of directly transmitted parasites.

Fish and their parasitic copepods exemplify a host-parasite relationship in which transmission is density-dependent. In fish farms, an unnaturally high density of salmon is shown to amplify transmission of sea lice (genera *Lepeophtheirus* and *Caligus*) to both farmed and wild fish (Krkošek et al. 2005; Sandvik et al. 2016). Sea lice populations further increase with sea temperatures due to faster lice development (Costello 2006; Sandvik et al. 2016). Thus, the potential for rapid population growth is enhanced during the warm summer months (Heuch et al. 2000) and is predicted to increase with increasing water temperatures (Godwin et al. 2021). However, apart from the interaction between fish farms, salmon and sea lice, there is little information on population dynamics of parasitic copepods from wild fish populations.

Copepods parasitic on gills ("gill lice", genus *Salmicola*) are less studied than sea lice, but can negatively affect oxygen uptake, reproduction, growth, and survival of wild fish (Gall et al. 1972; Sutherland and Wittrock 1985; Finley and Forrester 2003; Mitro 2016), and are a problem for freshwater aquaculture (Piasecki et al. 2004; Gunn et al. 2012). Infections in wild populations are usually low and may be self-limiting (McGladdery and Johnston 1988; Amundsen et al. 1997), but recent increases in infection incidences have called for a better understanding of factors driving the population dynamics of the parasite (Mitro and Griffin 2018). The development of *Salmincola* spp. is temperature dependent (Johnston and Dykeman 1987; Poulin et al. 1990a; Vigil et al. 2016), and recent mortalities of brook charr (*Salvelinus fontinalis*) in temperate areas of North America due to *Salmincola edwardsii* outbreaks are linked with increasing water temperature and fish densities (Mitro 2016; Mitro and Griffin 2018). In addition to density, another host property likely to play a key role in the dynamics of contact-transmitted parasites like copepods is host body size (Dogiel 1961; Poulin et al. 1991; Grutter and Poulin 1998; Boone and Quinlan 2019), which determines the surface area available for contact and attachment of infective stages.

A key measure to understand infection dynamics is the growth rate of parasite populations, i.e. the rate of increment or decrease in parasite population size across time. This is because although parasite population size should fluctuate with host density, parasite population growth rate may not. For example, at low sea lice densities, mating limitations produce a demographic Allee effect where low population size further limits population growth rate (Krkošek et al. 2012; Cox et al. 2017). A submaximal population growth rate due to mating limitation at low densities should also occur in other ectoparasitic copepods, such as gill lice. The severity of these Allee effects decreases with increasing fish size and temperature (Krkošek et al. 2012; Groner et al. 2014) and increased aggregation of parasites on individual fish can further alleviate demographic Allee affects if aggregation increases mating probabilities and does not induce host mortality (Krkošek et al. 2012; Cox et al. 2017).

In the present study, we utilize a unique long-term dataset spanning 32 years to investigate how fish density, size, habitat use, sex, and water temperature affect the population dynamics of *S. edwardsii* infecting Arctic charr (*Salvelinus alpinus*) in a subarctic lake. The density and size distribution of the host has fluctuated during the study period due to an intensive fish removal program in the 1980s and subsequent interspecific interactions with an increasing population of brown trout (*Salmo trutta*) (Persson et al. 2007; Amundsen et al. 2019). Brown trout is a predator and competitor of Arctic charr but is not a suitable host to *S. edwardsii* and therefore could reduce transmission to charr due to dilution effects (copepodids attempt to attach to brown trout but fail, e.g. Schmidt and Ostfeld 2001). Brown trout could also indirectly affect *S. edwardsii* through effects on the Arctic charr population by reducing charr density (Persson et al. 2007), or by increasing the aggregation of Arctic charr in profundal refuges (Mitro 2016; Jensen et al. 2017). At the parasite population level, we have identified four potential, non-exclusive, main effects that can drive long-term population dynamics of *S. edwardsii* in Arctic charr: Arctic charr density, Arctic charr size, water temperature and brown trout density. Together, these four factors capture what *a priori* should be the main drivers of *S. edwardsii* development rate and transmission success. We hypothesize that (1) fish size positively affects gill lice abundance, and (2) parasite abundance and transmission rate increases with host density and temperature, but decreases with brown trout density due to dilution effects. Finally, we hypothesize that (3) potential increases in Arctic charr size, temperature, and parasite aggregation from one year to the next also increase parasite population growth rates due to reduced Allee effects.

Materials and methods

Study site

Takvatn (69°07´N, 19°05´E) is a 15 km^2 large oligotrophic lake located in the Målselv River system in Troms county, northern Norway, and is usually ice-free from late May to November. The lake has a maximum depth of 80 meters and distinct littoral, profundal, and pelagic habitats. The littoral habitat normally extends to 15 m depth and covers approximately one third of the lake (Klemetsen and Knudsen 2013). There are only three fish species present in Takvatn; Arctic charr, brown trout and three-spined stickleback (*Gasterosteus aculeatus*). Of these, Arctic charr is the only suitable host for the parasitic copepod *Salmincola edwardsii*. In the early 1980s, a dense population of slow-growing Arctic charr dominated the fish community, with brown trout being nearly absent from the system. Between 1984 and 1991, an intensive culling effort with baited funnel traps removed ~720 000 (~35 tons) of Arctic charr from the lake, reducing the density by ~ 80% (Amundsen et al., 2019). The density of Arctic charr increased after termination of culling, but stabilized at lower densities likely due to predation from the increasing brown trout population (Fig. 1; Persson et al., 2007). The long-term effects of culling on the Arctic charr population include increased somatic growth rates and reduced infections of *Dibothriocephalus* spp. tapeworms, and are covered elsewhere (Amundsen et al. 2007, 2019; Persson et al. 2007; Henriksen et al. 2019).

Parasite life cycle, population size, and aggregation level

Salmincola edwardsii has a holarctic distribution and infects only charr species (genus *Salvelinus*) (Kabata 1969). It has a direct life cycle with a single host. Eggs are released into the water and hatch into free-living copepodids that must infect a suitable host. The life-span of the copepodid is temperature dependent, and the period of active swimming ranges from a few days up to two weeks (Conley and Curtis 1993). Copepodids rest on the lake floor and react to shadows and shock waves by actively swimming upwards (Poulin et al. 1990b). After successful attachment to the host the parasite goes through four larval stages (chalimus I – IV) that are separated by moults. Each stage typically lasts a few days, with the female stages taking longer time to develop (Conley and Curtis 1994). Adult males are much smaller than females, with a shorter lifespan that varies between 3 and 8 days at 13°C, and detach shortly after mating (Conley and Curtis 1994). The lifespan of female *S. edwardsii* is unknown, but a complete female life cycle for the related *Salmincola californiensis* takes 28 – 32 days at 11°C (Kabata and Cousens 1973). The preferred site of attachment is the gill region (Conley and Curtis 1994). We rarely observe copepods on the body surface or fins of the fish in Takvatn, although this has been reported from some systems (Fryer 1981).

For each year of data, we estimated values of mean intensity (average number of parasites *per* infected hosts), mean abundance (average number of parasites *per* host, including uninfected Arctic charr), the component population size (estimated as mean parasite abundance multiplied by the density of Arctic charr), and prevalence (proportion of infected hosts) of adult female *S. edwardsii*.

We also measured parasite aggregation on fish using Lloyd’s mean crowding (m_c) value (Lloyd 1967), calculated as:

$$\mathrm{m}_c = \mathrm{m} + \frac{v}{m},$$

where m is the average number of parasites on infected fish (mean intensity) and v is the variance of the mean intensity. This calculation is based on female parasites only, and we assume that males follow a similar pattern of aggregation among hosts.

Fish sampling, density, and body size

A total of 6893 Arctic charr were checked macroscopically for *S. edwardsii* on the gills and branchial cavity shortly after capture, and the total number of adult female copepods were counted. Arctic charr were sampled annually during the ice-free season from 1980 to 2018, except in 1998, but fish sampled from Takvatn prior to 1987 were not checked for *S. edwardsii* infection. Multimesh gillnets were placed in the littoral (<15 m depth), profundal (25 – 40 m depth) and pelagic (offshore, > 30 m depth) habitats of the lake, and fished overnight for approximately 12 hours. Each fish was wet-weighed (± 0.1 g), had its fork length measured (± 0.1 cm) and its sex determined. The lowest sample size any given year was 65 fish individuals in 2011. Most Arctic charr were caught in the littoral habitat (N = 4225) with fewer in the profundal (N = 2044) and pelagic (N = 624) habitats.

Arctic charr and trout densities were estimated by their catch-per-unit-effort (CPUE), calculated as number of fish caught per 100m^2 gillnet per night during the August sampling periods in each habitat (Fig 1). The total CPUE is the summary of CPUEs across all habitats, where the profundal CPUE is multiplied by two and the pelagic CPUE multiplied by three to account for their relative contribution to lake volume (Amundsen et al., 2007; Persson et al., 2007).

Fish size was measured as fish length and as surface area. Surface area was included as it has been suggested as more important than length for copepod transmission (Tucker et al. 2002; Frederick et al. 2017). Fish length corresponds to the fork length (cm) and surface area (cm^2) was estimated following the biomass-to-area conversion of 13.9 $M^{0.61}$ where M is wet-mass in grams (Frederick et al. 2017). This equation has originally been parameterized for another fish from the same family as Arctic charr, the Atlantic salmon (Frederick et al. 2017). Arctic charr length and surface area were highly correlated (Pearson's $r = 0.97$, $P < 0.001$, *d.f.*= 6891, see Online Resource S1), but differed somewhat in their ability to predict *Salmincola* infections and therefore both measurements are included in separate models (see Results and Online Resource S2).

Water temperature

Historical climatological data was assessed following a one-dimensional air-to-water-temperature model (see Smalås et al. 2020) based on measurements from a nearby meteorological station at Bardufoss Airport (~19 km from Lake Takvatn). The model was calibrated using water temperature data from Lake Takvatn for the years 1982, 1992, 1994, 1997, and 2017, and further validated using water temperature data in Takvatn from 2018 and 2019 (see Smalås et al. 2020 for more details on the methodology). Lake temperature is relatively constant during ice cover, and the largest among-year discrepancies in water temperature occur during summer above the thermocline (~10 meter depth in Takvatn), when elevated water temperatures likely impact *S. edwardsii* hatching and development (Kabata 1982). We therefore use the average water temperature from the top 10 meters of the water column over the months June, July, August and September as the predictor in our models (see below). The maximum temperature in the lake is around 14 °C during summer.

Data analyses

We first analysed how *S. edwardsii* abundance varied with Arctic charr size (hypothesis 1) using a generalized linear mixed model (GLMM) with fish surface area as a predictor variable. Parasite infections may differ among Arctic charr inhabiting different habitats (Siwertsson et al. 2016) and between sexes (Skarstein et al. 2005), and Arctic charr habitat and sex were therefore included as three- and two-level categorical predictors, respectively. Most fish are uninfected, causing an inflation of fish with zero parasites. To address this zero inflation in our data, we applied a negative binomial error structure to our model. Because we were interested in disentangling the effects of the above mentioned predictors on parasite abundance, we used years as random effects in our model.

We further tested how the association between *S. edwardsii* transmission rate and fish size was affected by Arctic charr density, brown trout density, and water temperature (hypothesis 2) using a combination of linear and logistic regression models. We used the force of infection as basis for our measure for transmission rate. The force of infection typically measures the time it takes for an uninfected individual to become infected with a parasite, and can be estimated from age-prevalence curves (McCallum et al. 2001). The rationale behind the method is that the time it takes for individuals to become infected with a parasite is proportional to the infection pressure in the environment. Arctic charr age and length were highly correlated in our material ($r = 0.85$, $P < 0.01$). For contact-transmitted parasites, size rather than age at infection might be a more suitable metric for infection pressure (Dogiel 1961). Furthermore, the somatic growth of Arctic charr (i.e. size at age) has changed over the last decades in Takvatn (Klemetsen et al. 2002; Amundsen et al. 2007). This could obscure the use of age-prevalence curves as a measure of infection pressure, and therefore size rather than age is more ecologically relevant for measuring transmission rate in this system. First, logistic regressions between Arctic charr length and parasite prevalence were computed for each year individually (Online Resource S3). From these models, we retrieved information on the fish length at which there was a 50% probability of Arctic charr being infected with *S. edwardsii*. In years with high transmission rates fish will likely become infected at smaller sizes and this measure can thus be considered as a proxy for the force of infection. We then tested if Arctic charr density, brown trout density, and water temperature affected fish length at 50% infection probability using linear regressions. This indirect approach was necessary as fish size and parasite counts have multiple measures for each year, whereas fish density and water temperature have only one measurement per year, thus yielding either pseudoreplicated data if multiple fish size and parasite count measures were included, or causing loss of information if only mean fish size and mean parasite abundance were used.

Following the above individual-level analyses, we shifted our focus to the parasite population, and tested the effects of Arctic charr density, body size, brown trout density, and water temperature on *S. edwardsii* mean abundance using multiple regression analysis (model 1 – current data). We also tested the effects of the predictors using one-year-lagged data to check for potential delayed effects. We included these variables in a separate model (model 2 – lagged data) to avoid overfitting issues and collinearity between lagged and non-lagged values of fish density and temperature. We interpolated values for the missing year 1998 by using the function "Na.spline" from the Zoo package in R (Zeileis and Grothendieck 2005). We checked for residual autocorrelation in the model using the Durbin-Watson test. When autocorrelation was detected, we either fitted an autoregressive term (AR1) or a moving average term (MA1) to a generalized least squares (GLS) model, following the "auto.arima" function from the forecast package (Hyndman and Khandakar 2008). We inspected diagnostic plots for all regression models.

Because the CPUEs of Arctic charr and brown trout may be distinct across habitats (littoral, pelagic, and profundal), averaging Arctic charr and brown trout CPUEs within the lake might lead to imprecise estimates of fish densities. We therefore additionally analysed the effect of the aforementioned predictor variables on *S. edwardsii* abundance using data from the littoral zone only. This was not done for the two other habitats, as sample sizes were not large enough.

To test how changes in fish population structure across years affected parasite population growth (hypothesis 3), we first explored the temporal patterns of host and parasite population structure using autocorrelation functions (ACF) of *S. edwardsii* mean abundance and component population size, Arctic charr density, and brown trout density. The shape of the

ACF provides insights into the density-dependence, stationarity and periodicity of population dynamics (Turchin and Taylor 1992; Ryo et al. 2019). Significant lags suggest dependence on population sizes in previous years. The temporal trend between population size and year is provided as Pearson's correlations. We then tested how temporal changes in Arctic charr body size, brown trout density, temperature and parasite aggregation affected population growth of *S. edwardsii*.

We calculated *S. edwardsii* population growth rate as the intrinsic rate of increase (r_t):

$$r_t = \ln(N_t/N_{t-1}),$$

where N_t is the component population size at year t (Turchin and Taylor 1992; Lester et al. 2017). As population growth rate (r) necessarily assumes a change from year t-1 to t, we modelled r_t as a response of similar t/t-1 changes (∆) in Arctic charr body size, brown trout density, summer water temperature and parasite mean crowding. Arctic charr density was not included as a predictor variable as it is nested in the measure of parasite population size (estimated as mean parasite abundance × Arctic charr density).

Brown trout could indirectly influence the parasite population through changes in the habitat use or size distribution of Arctic charr. We therefore analysed if there was a correlation between brown trout density in year t, t-1and t-2 and the total density Arctic charr using Pearson's correlation. As brown trout is generally found in the littoral habitat only, we specifically tested if brown trout density in the littoral zone was related to Arctic charr density in each of the three habitats using Pearson's correlations. Finally we checked if there was a correlation between brown trout density and Arctic charr length.

Results

The overall prevalence of *S. edwardsii* throughout the 32-year study period was of 17.4 %, but parasite prevalence fluctuated annually, from a minimum of 3.9 % (2007) to a maximum of 43.8 % (2017) (for years see Online Resource Fig. S4). Mean parasite intensity also varied across years, ranging between 1.1 (2003) and 8.1 (2018). Likewise, fish densities fluctuated throughout the study period. The density of Arctic charr was highest in the littoral and profundal habitats whereas brown trout mainly occupied the littoral habitat (Fig. 1). Overall, we did not find a clear effect of total brown trout density on the total density of Arctic charr, but we found a positive relationship between brown trout density in the littoral habitat and Arctic charr density in the profundal habitat ($r = 0.47$, $P < 0.01$). There was no correlation between brown trout density and the mean length of Arctic charr ($r = 0.07$, $P = 0.70$).

S. edwardsii **abundance increases with fish length**

We found a clear positive relationship between Arctic charr body size (length) and *Salmincola edwardsii* abundance (Z = 36.6, $P < 0.01$, Table 1), and a tendency for Arctic charr caught in the profundal habitat to have more parasites (Z = 1.9, $P = 0.06$, Table 1). We did not find any effect of fish sex on parasite abundance ($P = 0.47$). Fish length explained more variation in abundance than surface area ($\Delta R^2 = 5.6$, Online Resource S2). The fixed effects length and habitat explained 42.7 % of the variation in *S. edwardsii* abundance, with the random effect year explaining an additional 6.5 % of the variation (Table 1).

Arctic charr become infected with *S. edwardsii* at smaller sizes in years with higher densities of brown trout

Our measure of infection pressure, fish length at which there was a 50% probability of parasite infection, varied from 254 mm (2016) to 391 mm (2003) (Fig. 2). The logistic regressions describing this relationship were significant for all years except 2000, 2006, and 2009, which were excluded from subsequent linear regression analysis. Brown trout density was the only significant predictor of the length at 50% probability of infection (linear regression, P = 0.015, adjusted R^2 = 0.175). The slope of the association was negative, indicating that in years with higher densities of brown trout, Arctic charr became infected with *S. edwardsii* at smaller sizes (Fig. 2). There was no effect of Arctic charr density or temperature in the current or previous year on infection pressure (all $P > 0.63$).

Fish surface area predicted annual *S. edwardsii* mean abundance with an additional negative effect of Arctic charr density and positive effect of summer temperature in the previous year

Mean Arctic charr surface area explained much of the variation in mean parasite abundance in year t (Fig. 3, Table 2). Surface area was a better predictor of mean parasite abundance than mean fish length (lower AIC, Online Resource S2). An increase of 10 cm^2 in surface area (range 124 – 347 cm^2) on average increased mean parasite abundance by 0.06 (range: 0.06 – 2.50). We also detected a negative effect of Arctic charr density in year t (Table 2) with an increase of 1 in charr CPUE (range 7.7 – 34.6) decreasing mean abundance by 0.02. Temperature and brown trout density had positive and negative effects on parasite mean abundance, respectively, but those effects were small. In the lagged model there was a positive effect of brown trout density in year t-1 on mean abundance in year t (Table 3). An increase of

1 in brown trout CPUE (range: 0.03 – 12.6) in year *t*-1 increased mean parasite abundance by 0.10. There was a positive effect of water temperature in year *t*-1, but the confidence interval included zero. When analysing data from the littoral habitat only, our results indicated that mean parasite abundance increased with Arctic charr surface area in year *t* and brown trout density in year *t*-1 and decreased with Arctic charr length in year *t*-1 (Online Resource S5).

Autocorrelation plots revealed different temporal dynamics for the *S. edwardsii* and Arctic charr populations

Our analysis of temporal autocorrelation indicated a dependency of mean parasite abundance and component population size on their values in previous year (Fig. 4). Brown trout density was autocorrelated with its own densities during the 3 preceding years (Fig. 4). *Salmincola edwardsii* mean abundance, component population size, and brown trout density displayed decreasing autocorrelation values that became increasingly negative at long lags, suggesting a gradual trend in the mean over time (Turchin and Taylor 1992). Accordingly, Pearson correlations indicated a temporal increase in means for all three time series (mean abundance: $r = 0.43$, $P = 0.014$, component population size: $r = 0.41$, $P = 0.021$, brown trout: $r = 0.70$, $P < 0.001$). The ACF of the Arctic charr population on the other hand, displayed periodic oscillations around a constant mean (Fig. 4), and there was no trend with time ($r = 0.01$, $P = 0.952$).

Yearly changes in fish surface area predict *S. edwardsii* population growth rate with additional effects of brown trout density and mean parasite crowding

We found a clear positive effect of yearly change in Arctic charr surface area on *S. edwardsii* population growth rate, with surface area alone explaining 73 % of the variation (Fig.

3). There were additional positive effects of brown trout density and mean crowding, which explained an additional 9 % of the variation in parasite population growth (Online Resource Table S2.3). There was no effect of water temperature on parasite population growth rate (P = 0.942).

Discussion

Fish body size was the strongest predictor of parasite population size and population growth. Contrary to current host-parasite models, we did not find any positive effects of host density on the transmission rate of the copepod parasite, and the host and parasite populations fluctuated independently of one another. Instead, the presence of the non-host intraguild predator brown trout was associated with higher abundance of gill lice in Arctic charr, possibly due to predator-avoidance strategies of the Arctic charr. Parasite populations of freshwater fish are suggested to be unregulated and unstable over time (Kennedy 2009), but the *S. edwardsii* time series provides evidence of year-to-year predictability of a parasite with a short life span. The present study contributes to our understanding of long-term drivers of parasite population dynamics in wild fish populations.

Individual heterogeneity in parasite infections was related to host body size as hypothesized. The abundance of ectoparasites generally increases with host body size, as larger hosts provide more living space for parasites and are larger targets for infective parasitic stages (Poulin and Rohde 1997; Grutter and Poulin 1998). For gill lice, parasite abundance may additionally increase with fish body size because larger fish have higher ventilation volumes (Poulin et al., 1991). The individual heterogeneity in parasite infections due to fish size translated into population level changes in parasite mean abundance, which clearly followed changes in the size distribution of the fish population across the years.

The length at which fish became infected with gill lice is a proxy for infection pressure, and thus an important measure of host-parasite dynamics. Here, the length of first infection varied across years, and was not related to water temperature nor host density. However, contrary to our hypothesis that brown trout would dilute parasite transmission to Arctic charr, we found that charr became infected at smaller sizes in years with higher densities of brown trout. Mitro (2016) suggested that an increase in brown trout density increased *S. edwardsii* infections in brook charr by inducing shifts in brook charr behaviour and habitat utilization that facilitated transmission. A similar mechanism could explain our results from Takvatn, as the density of Arctic charr in the profundal habitat was higher in years with high densities of brown trout, leading to higher infections of gill lice in that habitat. The resting behaviour of copepodids on the lake floor and their longer survival times at cold temperatures might facilitate transmission in the profundal habitat (Poulin et al. 1990b; Conley and Curtis 1993). The mean abundance of gill lice was also higher in years with more brown trout. This shows how interspecific interactions between host and non-host affect parasite population dynamics. Nonetheless, the direction and magnitude of such effects are dependent on the nature of the infection. For trophically transmitted tapeworm species (*Dibothriocephalus* spp.), brown trout has contributed to dilute infections of Arctic charr in Takvatn (Henriksen et al. 2016, 2019).

Contrary to our second hypothesis, we found no evidence of a positive relationship between host density and *S. edwardsii* mean abundance. In fact, there was a negative association between Arctic charr density and the mean abundance of gill lice. Spatial studies have reported a similar negative pattern between parasite abundance and host density (Lagrue and Poulin 2015; Buck and Lutterschmidt 2017). The encounter-dilution effect, where infection risk decreases with group size due to more available hosts per parasite, is suggested to explain the negative association between parasite abundance and host density of a trematode parasite infecting centrarchid fishes (Buck and Lutterschmidt 2017). Similarly, the intensity of infection decreased with host density for contact-transmitted parasites infecting invertebrates and fish in New Zealand lakes (Lagrue and Poulin 2015). Long-term studies of helminths in voles (Haukisalmi and Henttonen 1990) and acanthocepalans in seals (Valtonen et al. 2004) did not show strong links between temporal changes in host densities and parasite population dynamics**.** The population dynamics of *S. edwardsii* were trend-stationary in contrast to the cyclic dynamics of the Arctic charr population (Turchin and Taylor 1992; Ryo et al. 2019), providing further evidence that factors independent of host density regulate the parasite population. Although host density is an integral part of epidemiological models, empirical evidence of its importance in regulating parasite populations of hosts fluctuating at natural densities remains ambiguous.

The prevalence and abundance of gill lice were generally low as expected, and we hypothesized that Allee effects might limit parasite population growth rate. Such effects should be less severe as fish size increases (Krkošek et al. 2012), and changes in fish surface area predicted much of the variation in parasite population growth rates. There was also a positive effect of parasite aggregation as hypothesized. The encounter rates between male and female parasites on their hosts is essential for the overall transmission function (Orlofske et al. 2018). Hence, if increases in aggregation resulting from increases in fish size facilitate encounter rates between parasites, this might be a mechanism explaining the increase in population growth rate with size. In sea lice, females produce chemical cues that attract males (Ingvarsdóttir et al. 2002; Pino-Marambio et al. 2007). This could be a mechanism to increase the per-parasite encounter rate and parasite aggregation. An important limitation to our study is that we have no information on the presence of male lice, as these leave the host shortly after mating. We therefore cannot estimate the true degree of mating limitations in our system.

Warmer water temperatures should increase the hatching success and development rates of *Salmincola* spp. resulting in more generations per year (Poulin et al. 1990a; Vigil et al. 2016). We did not observe any clear effects of temperature on parasite mean abundance or transmission, and temperature did not drive the growth rate of the parasite population. The buffer capacity towards changes in temperature is large for a deep lake like Takvatn. Differences in lake morphometry and their influence on abiotic conditions affect parasite transmission to other charr species (Filion et al. 2019), and we might have observed a larger effect of temperature in a shallower lake. Furthermore, Arctic charr somatic growth rates increase with temperature (Smalås et al. 2020). This should manifest in higher *Salmincola* transmission rates, but such effects occur over the lifespan of the host and would not be detected in the present study. Altogether, temperature can impact the parasite population directly through effects on parasite development and indirectly by increasing host size.

Parasitic copepods adversely affect wild salmonid populations (Thorstad et al. 2015; Mitro 2016; Bøhn et al. 2020). Recent increases in gill lice infections have called for a better understanding of their population dynamics (Mitro and Griffin 2018; White et al. 2020). Our results suggest that host size determines parasite abundance and that yearly increments in host size are more important than host density in regulating the *S. edwardsii* population over time. Individual growth rates of salmonids are inversely related to fish density (Amundsen et al. 2007; Matte et al. 2020). Consequently, for contact-transmitted parasites, there might exist a counterintuitive negative relationship between fish density and parasite population size. However, the effects of fish density and temperature on somatic growth rate slowly manifest over several years, and we could not detect their potential indirect effects on the parasite population in the present study. Overall, our study supports that individual traits affecting infection risk determine long-term epidemiological patterns at the population level (McDonald et al. 2018). There is a critical density threshold of hosts needed for successful parasite transmission (Dallas et al. 2018). Nevertheless, for wild host populations fluctuating above this threshold, density does not appear to be the main driver of parasite transmission.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Tables

Table 1. Results from generalized linear mixed effects model with negative binomial errors predicting *S. edwardsii* abundance in Lake Takvatn. Length and habitat of individual Arctic charr are fixed effects and sampling year is the random effect.

	S. edwardsii abundance		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.19	0.16 – 0.23	**<0.001**
Length	3.43	3.21 – 3.67	**<0.001**
Habitat [Profundal]	1.18	0.99 – 1.41	0.060
Habitat [Pelagic]	0.89	0.70 – 1.12	0.329
Random Effects			
σ^2	1.74		
$\tau_{00\ \mathrm{YEAR}}$	0.22		
ICC	0.11		
N_{YEAR}	31		
Observations	6893		
Marginal R^2 / Conditional R^2	0.427 / 0.493		

Table 2. Results from generalized least squares with MA1 correlation structure predicting *S. edwardsii* mean abundance in year *t*.

	***S. edwardsii* mean abundance**		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.46	-0.21 – 1.12	0.190
Mean surface area $_{\text{year } t}$	0.01	0.00 – 0.01	**<0.001**
Arctic charr density $_{\text{year } t}$	-0.02	-0.04 – -0.01	**0.012**
Brown trout density $_{\text{year } t}$	0.04	-0.01 – 0.08	0.114
Water temperature $_{\text{year } t}$	-0.09	-0.19 – 0.01	0.085
Observations	32		

Table 3. Results from generalized least squares with AR1 correlation structure predicting *S. edwardsii* mean abundance in year *t* with lagged predictors.

	S. edwardsii mean abundance		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.07	-2.23 – 2.08	0.946
Mean surface area $_{\text{year } t\text{-}1}$	-0.00	-0.00 – 0.00	0.116
Arctic charr density $_{\text{year } t\text{-}1}$	-0.02	-0.05 – 0.01	0.169
Brown trout density $_{\text{year } t\text{-}1}$	0.10	0.03 – 0.17	**0.010**
Water temperature $_{\text{year } t\text{-}1}$	0.19	-0.01 – 0.39	0.074
Observations	31		

Figures

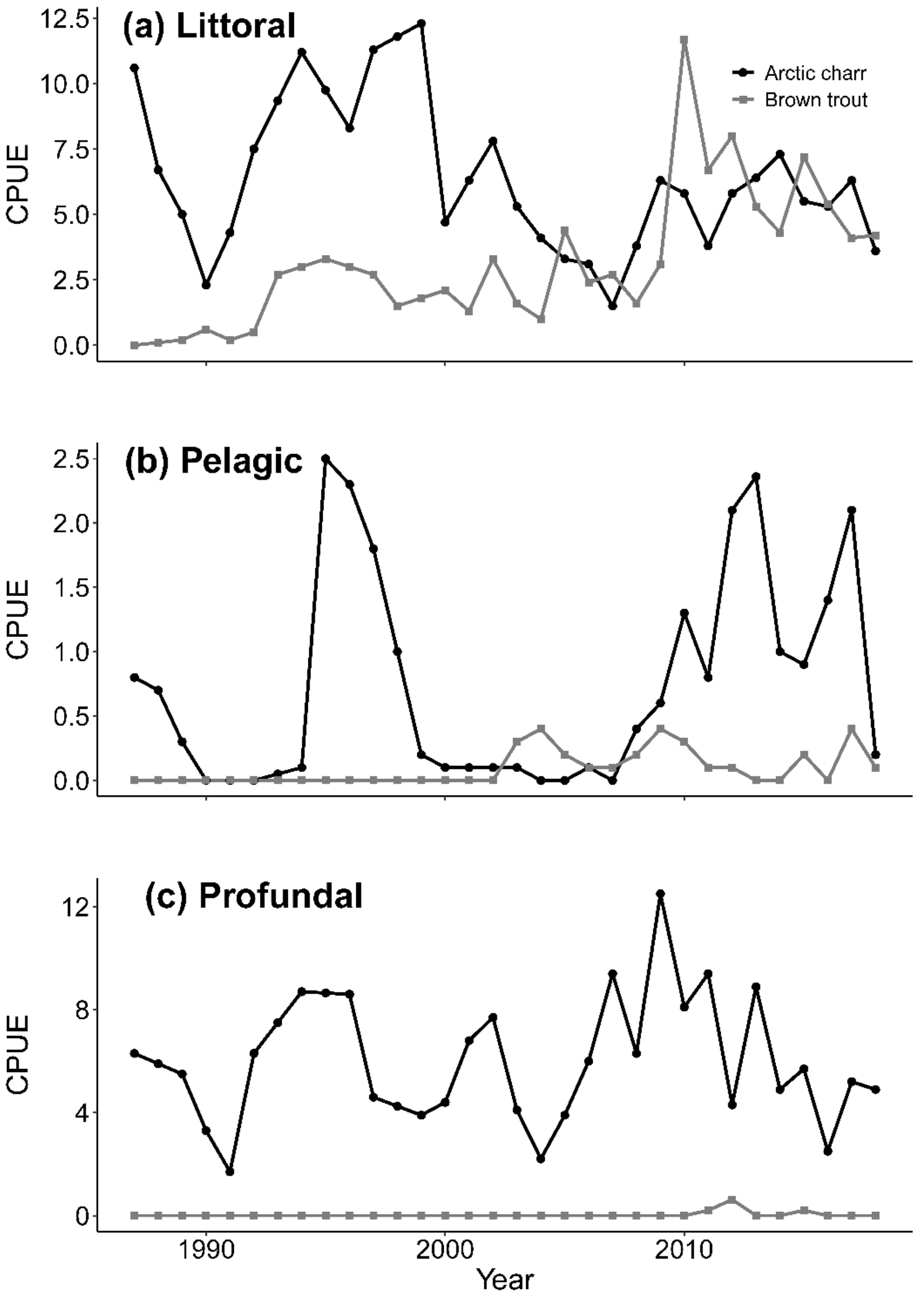

Fig. 1 Density developments (CPUE) of Arctic charr (black circles) and brown trout (grey sqaures) in the (a) littoral, (b) pelagic and (c) profundal habitats in Lake Takvatn from 1987 until 2018

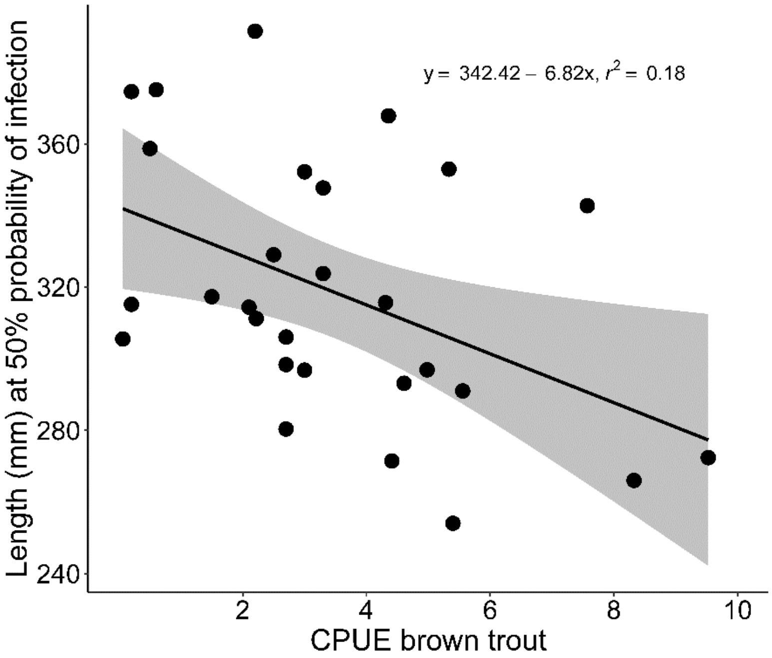

Fig. 2 Length at which Arctic charr has a 50 % probability of infection with *S. edwardsii* (retrieved from logistic regressions) as a function of brown trout density in Lake Takvatn for all years where the infection probability ~ length slope was statistically significant (*P* < 0.05, Online Resource S3). The shaded area represents the 95 % confidence interval

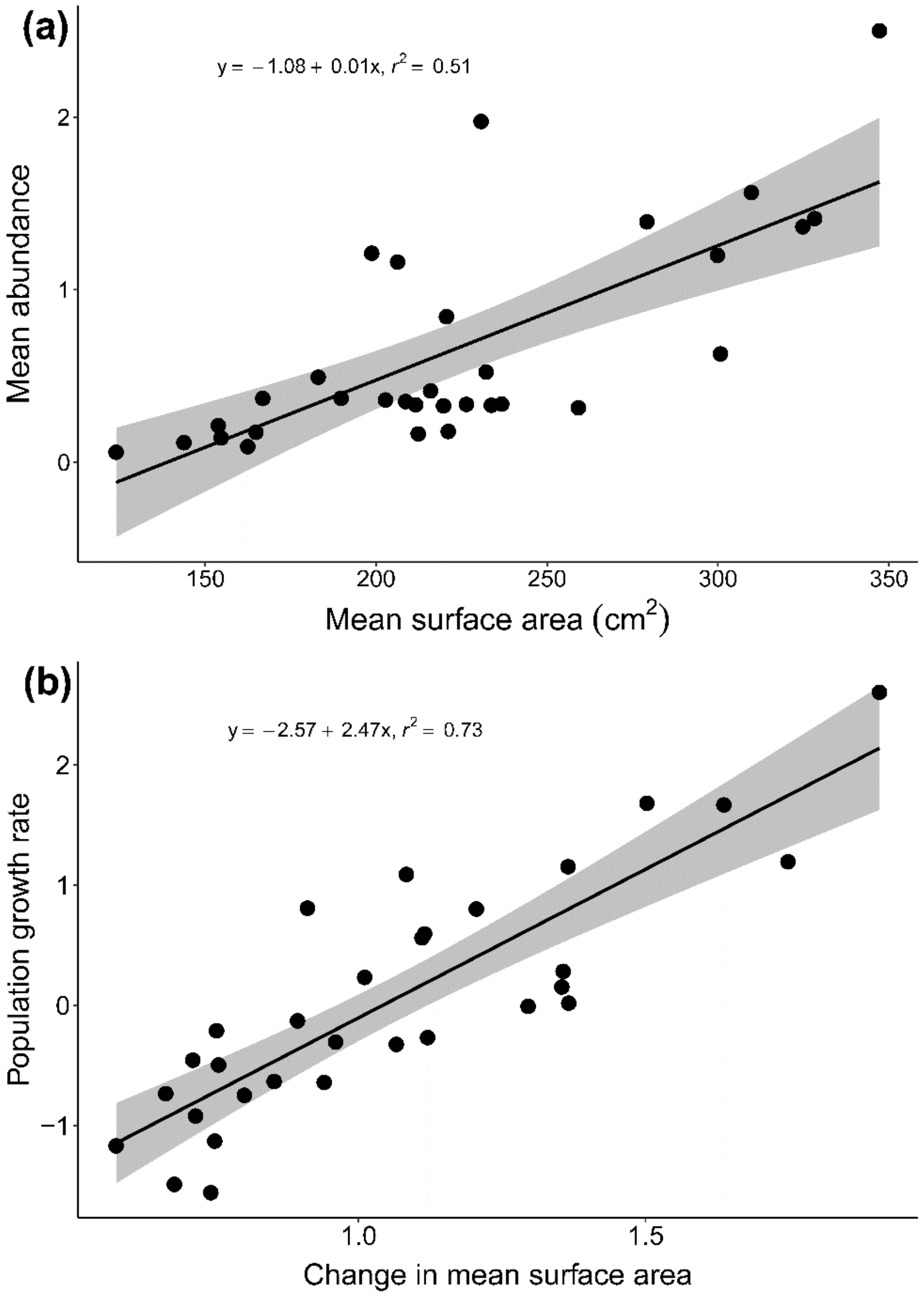

Fig. 3. (a) Mean abundance of *S. edwardsii* as a function of mean body surface area of Arctic charr in every year sampled from 1987 to 2018 in Lake Takvatn. (b) *Salmincola edwardsii* population growth rate from year *t*-1 to *t* as a function of the relative change in mean body surface area from year *t*-1 to *t*. The shaded area represents the 95 % confidence interval

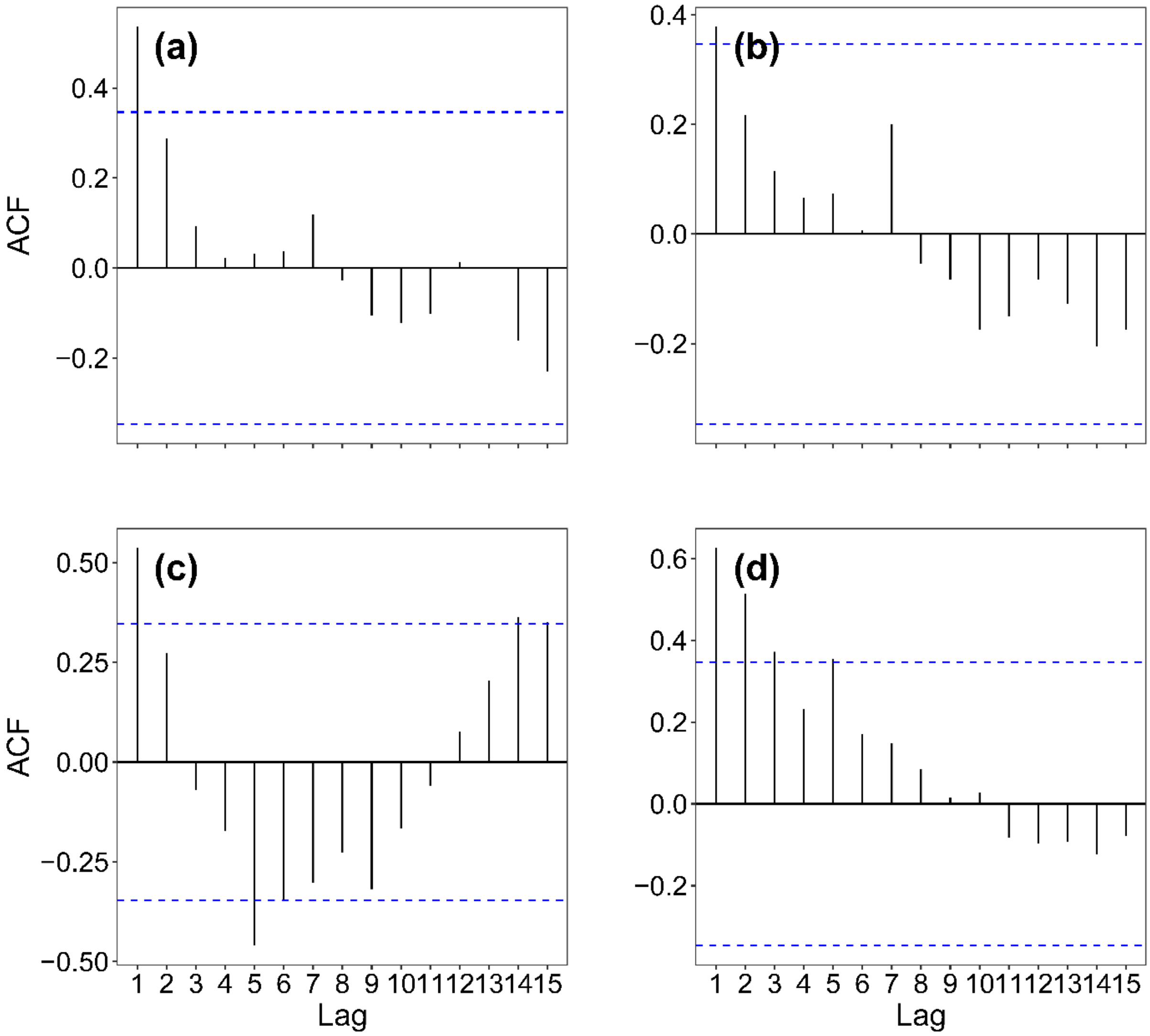

Fig. 4 Autocorrelation functions (ACF) for the time series of *S. edwardsii* (a) mean abundance and (b) component population size, (c) Arctic charr density, and (d) brown trout density. Dotted lines indicate where the autocorrelation is statistically significant ($P < 0.05$)

Electronic Supplementary Material

Long-term ectoparasite population dynamics driven by changes in host size but not host density or temperature

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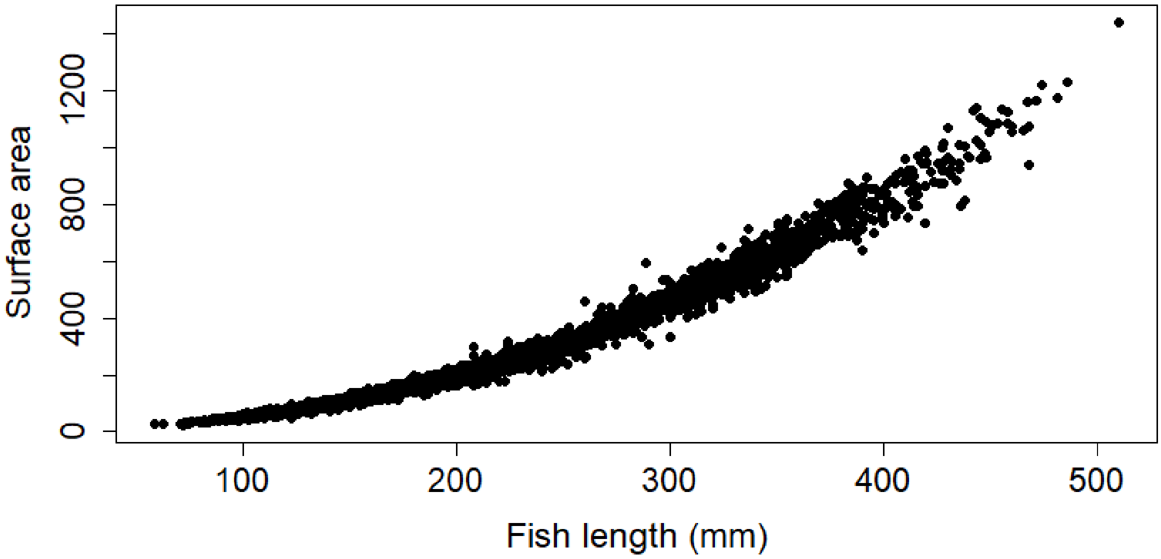
Online Resource S1 | The association between fish length and surface area



Supplementary Figure S1. The association between fish length and surface area (cm^2) for all 6893 Arctic charr in the dataset.

Online Resource S2 | Models with surface area versus length as predictors

The model with surface area explained less of the variation in the abundance of *S. edwardsii* (Table S2.1) than the model with length (see results in original manuscript). The AIC for the model in table S1 was 8871 compared to 8801 for the model presented in the results of the original manuscript. The conditional R^2 was 5.6 higher for the model with surface area as a predictor compared to length.

For the models predicting *S. edwardsii* mean abundance and growth rate, mean surface area was a better predictor than mean length. The difference in AIC was 2.3 for mean abundance and 8.0 for growth rate (tables S2.2 and S2.3, S2.4, respectively).

Supplementary Table S2.1. Results from generalized linear mixed effects model with negative binomial errors predicting *S. edwardsii* abundance in Lake Takvatn. Length and habitat of individual Arctic charr are fixed effects and sampling year is the random effect.

	S. edwardsii abundance		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.21	0.18 – 0.26	**<0.001**
Surface area	2.98	2.80 – 3.17	**<0.001**
Habitat [Profundal]	1.07	0.90 – 1.27	0.426
Habitat [Pelagic]	0.98	0.77 – 1.23	0.843
Random Effects			
σ^2	1.76		
τ_{00} YEAR	0.19		
ICC	0.10		
N YEAR	31		
Observations	6893		
Marginal R^2 / Conditional R^2	0.375 / 0.437		

Supplementary Table S2.2. Results from generalized least squares with MA1 correlation structure predicting *S. edwardsii* mean abundance in year *t*.

	***S. edwardsii* mean abundance**		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-1.16	-2.08 – -0.23	**0.021**
length	0.01	0.01 – 0.02	**<0.001**
cpue_charr	-0.02	-0.04 – -0.01	**0.011**
cpue_trout	0.04	-0.01 – 0.09	0.139
summer_temp	-0.06	-0.17 – 0.04	0.259
Observations	32		

Supplementary Table S2.3. Multiple regression predicting parasite population growth rate, ln(N_t/N_{t-1}). Predictors are expressed as t/t-1 changes (Δ).

	S. edwardsii population growth rate		
Predictors	*Estimates*	*CI*	*P*
(Intercept)	-2.51	-4.35 – -0.66	**0.010**
Δ Mean surface area	2.01	1.47 – 2.54	**<0.001**
Δ Brown trout density	0.14	-0.01 – 0.28	0.062
Δ Mean parasite crowding	0.17	0.06 – 0.27	**0.002**
Δ Water temperature	-0.06	-1.62 – 1.50	0.942
Observations	31		
R^2 / R^2 adjusted	0.843 / 0.819		

Supplementary Table S2.4. Multiple regression predicting parasite population growth rate, $\ln(N_t/N_{t-1})$. Predictors are expressed as t/t-1 changes (Δ).

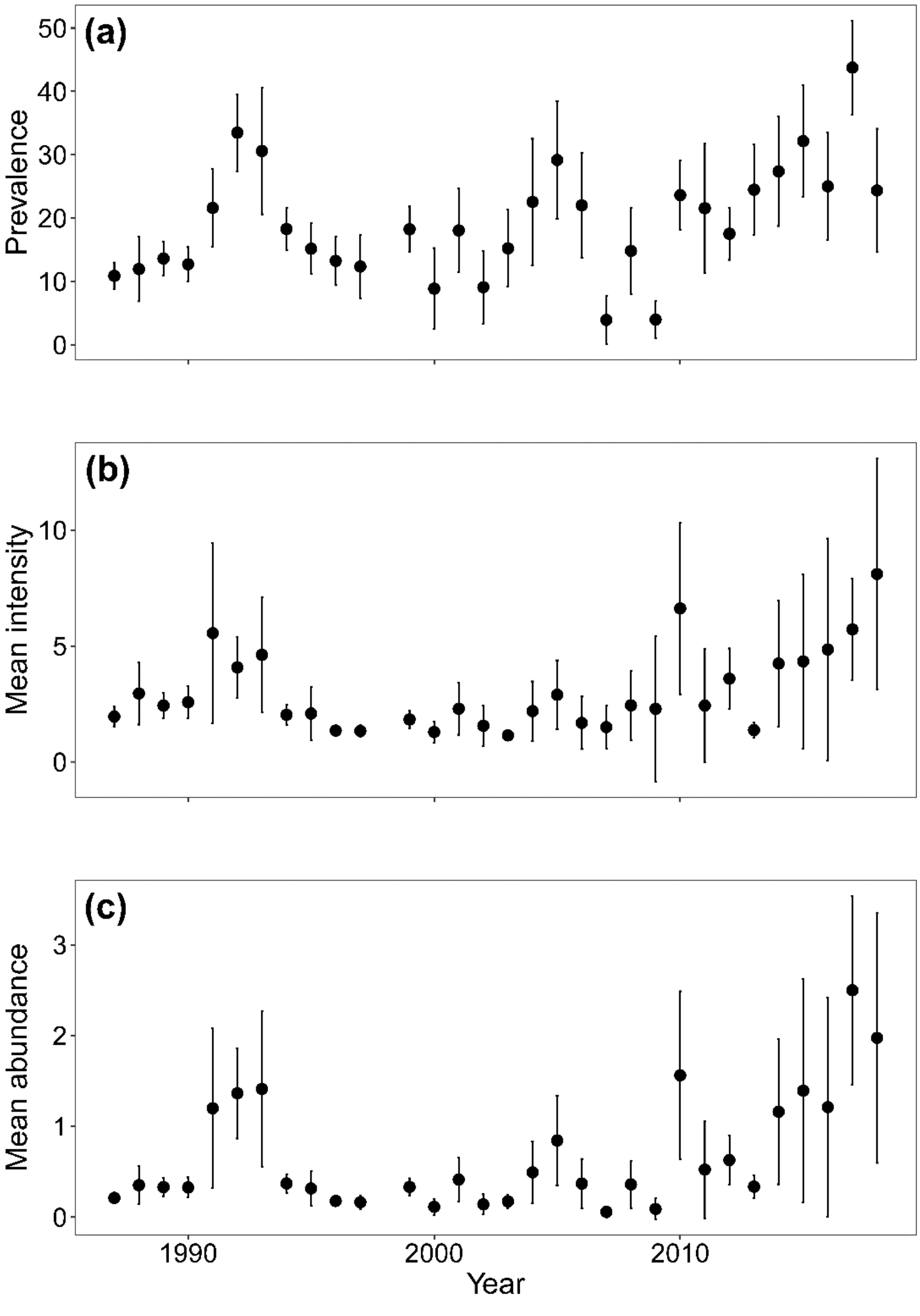
	S. edwardsii population growth rate		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.20	-2.19 – 1.80	0.840
Δ Mean length	0.02	0.01 – 0.03	**<0.001**
Δ Brown trout density	0.15	-0.03 – 0.32	0.098
Δ Mean parasite crowding	0.20	0.08 – 0.33	**0.002**
Δ Water temperature	-0.31	-2.20 – 1.58	0.736
Observations	31		
R^2 / R^2 adjusted	0.768 / 0.732		

Online Resource S3 | Logistic regression models between fish length and *Salmincola edwardsii* prevalence

Supplementary Table S3. Summary for logistic regression models of probability of infection with *Salmincola edwardsii* vs Arctic charr length for individual years. Asterisks indicate levels of significance (*, P < 0.05, **, P < 0.01, *** P < 0.001, no asterisk = P > 0.05). SE = standard error.

Year	Intercept ± SE	Length ± SE	Z-value inter-cept	Z-value length	N fish	Length at 50 % infection probability
1987	-5.453 ± 0.44 ***	0.018 ± 0.00 ***	-12.528	8.487	828	305.52
1988	-7.219 ± 1.16 ***	0.023 ± 0.00 ***	-6.242	5.217	159	315.25
1989	-4.654 ± 0.41 ***	0.012 ± 0.00 ***	-11.377	7.935	617	375.12
1990	-4.668 ± 0.40 ***	0.012 ± 0.00 ***	-11.755	8.228	590	374.61
1991	-4.501 ± 0.71 ***	0.013 ± 0.00 ***	-6.301	5.207	176	358.61
1992	-3.674 ± 0.47 ***	0.012 ± 0.00 ***	-7.9	7.316	236	306.06
1993	-5.304 ± 1.01 ***	0.018 ± 0.00 ***	-5.269	5.019	85	296.81
1994	-3.395 ± 0.31 ***	0.010 ± 0.00 ***	-10.779	6.894	520	347.69
1995	-5.051 ± 0.78 ***	0.014 ± 0.00 ***	-6.447	4.471	310	352.27
1996	-9.813 ± 1.62 ***	0.035 ± 0.01 ***	-6.063	5.184	302	280.37
1997	-6.584 ± 1.32 ***	0.021 ± 0.01 ***	-4.974	3.796	170	317.32
1999	-4.751 ± 0.49 ***	0.015 ± 0.00 ***	-9.654	7.343	450	314.39
2000	-3.545 ± 1.17 *	0.007 ± 0.01	-3.035	1.173	79	491.75
2001	-4.430 ± 0.73 ***	0.014 ± 0.00 ***	-6.063	4.658	133	323.79
2002	-5.219 ± 1.13 **	0.016 ± 0.01 **	-4.611	2.944	99	329.06
2003	-3.176 ± 0.78 ***	0.008 ± 0.00 *	-4.082	2.048	138	391.47
2004	-3.442 ± 1.05 **	0.012 ± 0.01 *	-3.262	2.244	71	296.91
2005	-2.776 ± 0.69 ***	0.009 ± 0.00 **	-4.001	2.991	96	298.36
2006	-2.494 ± 0.74 ***	0.007 ± 0.00	-3.383	1.819	100	360.91
2007	-7.640 ± 2.23 ***	0.025 ± 0.01 *	-3.423	2.411	102	311.19
2008	-3.984 ± 0.78 ***	0.011 ± 0.00 ***	-5.096	3.363	108	367.83
2009	-4.119 ± 1.21 ***	0.005 ± 0.01	-3.398	0.851	176	785.00
2010	-4.394 ± 0.62 ***	0.013 ± 0.00 ***	-7.111	5.678	233	342.74
2011	-9.211 ± 2.52 ***	0.034 ± 0.01 ***	-3.661	3.448	65	272.38
2012	-6.001 ± 0.72 ***	0.017 ± 0.00 ***	-8.375	6.833	331	352.96
2013	-3.476 ± 0.70 ***	0.011 ± 0.00 ***	-4.989	3.71	143	315.66
2014	-3.961 ± 0.71 ***	0.015 ± 0.00 ***	-5.557	4.719	106	266.01
2015	-3.414 ± 0.63 ***	0.012 ± 0.00 ***	-5.381	4.79	112	291.00
2016	-4.702 ± 0.81 ***	0.019 ± 0.00 ***	-5.779	4.776	104	254.04
2017	-4.094 ± 0.64 ***	0.015 ± 0.00 ***	-6.365	6.332	176	271.45
2018	-4.511 ± 0.95 ***	0.015 ± 0.00 ***	-4.756	4.05	78	293.15

Online Resource S4 | Prevalence, mean intensity and mean abundance of *Salmincola edwardsii* in Arctic charr over the study period



Supplementary Fig. S4. (a) Prevalence, (b) mean intensity and (c) mean abundance of *Salmincola edwardsii* infecting Arctic charr in Lake Takvatn from 1987 to 2018. Error bars indicate 95 % confidence intervals.

Online Resource S5 | Analyses restricted to fish caught in the littoral habitat.

Tables S5.1 and S5.2 show predictions for littoral fish only. Mean surface area was a better predictor than mean length (AIC of 67.0 versus 69,9, respectively) in the current model, whereas the oppositce was true for the lagged model (86.0 versus 84.0).

Supplementary Table S5.1. Results from generalized least squares with AR1 correlation structure predicting *S. edwardsii* mean abundance in year *t* for fish caught in the littoral zone.

	S. edwardsii mean abundance littoral		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.27	-1.61 – 2.15	0.782
Mean surface area $_{\text{year } t}$	0.01	0.00 – 0.01	**<0.001**
Arctic charr density $_{\text{year } t}$	0.01	-0.05 – 0.07	0.767
Brown trout density $_{\text{year } t}$	-0.01	-0.08 – 0.06	0.781
Water temperature $_{\text{year } t}$	-0.11	-0.28 – 0.06	0.202
Observations	32		

Supplementary Table S5.2. Results from generalized least squares with AR2 correlation structure predicting *S. edwardsii* mean abundance in year *t* for fish caught in the littoral zone with lagged predictors.

	S. edwardsii mean abundance littoral		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	2.31	0.15 – 4.47	**0.046**
Mean surface area $_{\text{year } t\text{-1}}$	-0.01	-0.01 – -0.00	**<0.001**
Arctic charr density $_{\text{year } t\text{-1}}$	-0.05	-0.15 – 0.04	0.253
Brown trout density $_{\text{year } t\text{-1}}$	0.13	0.04 – 0.21	**0.006**
Water temperature $_{\text{year } t\text{-1}}$	-0.02	-0.22 – 0.19	0.885
Observations	31		

Paper III

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Fish age and population size structure affect the abundance and aggregation of a long-lived nematode parasite.

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Fish age and population size structure affect the abundance and aggregation of a long-lived nematode parasite

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Abstract

Abundance and aggregation assess parasite population size and the spatial distribution of parasite individuals among hosts. Cross-sectional studies examining relationships among parasite abundance, aggregation, and host age have provided insight to mechanisms that structure parasite population dynamics. However, the temporal stability of this association has received little attention. Here, we evaluate potential long-term drivers of parasite abundance and aggregation over a three-decade study period, using Arctic charr and a long-lived parasitic nematode as our host-parasite association. Specifically, we explore the distribution of parasites among age classes and the interrelationships between temporal changes in host age, parasite abundance and parasite aggregation. Two recently proposed methods for analysing parasite aggregation, the Hoover index and a measure based on feasible set theory, showed similar results. Parasite abundance increased with host age and size, which in turn reduced parasite aggregation, demonstrating an indirect negative effect of host age on parasite aggregation via parasite abundance. This negative association was temporally stable despite periodic fluctuations in infection pressure. Heterogeneity in fish body size and feeding mode further increased parasite aggregation, but these effects diminished when accounting for host population age structure. The demography and ontogenetic dietary shifts of Arctic charr have shifted over time due to reduced intraspecific competition and enhanced interactions with brown trout, which appears to be the most important determinant of the revealed temporal variations in parasite transmission. Following a period of oscillations, we observed stability in host-parasite dynamics, possibly due to regulatory processes acting on parasite infrapopulations or simply due to ecosystem stability.

Keywords: parasite aggregation, population ecology, host-parasite, long-term study, *Cystidicola farionis, Salvelinus alpinus*

Introduction

A central aim in ecology is to understand the abundance and distribution of populations across space and time. The aggregated distribution of parasites among hosts, where a large proportion of the parasite population resides in a small proportion of the host population, is a near universal feature of parasite populations (Shaw and Dobson 1995; Poulin 2007a). Parasite aggregation affects the evolution, stability and dynamics of both host and parasite populations (Anderson and May 1978; May and Anderson 1978). Whereas parasite mean abundance provides an estimate of parasite population size (Bush et al. 1997), aggregation provides a measure for how parasite individuals are distributed among hosts. Taken together, mean abundance and aggregation provide information on the size and patch use of parasite populations, which are two key measures in general population ecology. Importantly, differences in abundance and aggregation among different subsets of the host population provide clues into whether density-dependent mechanisms regulate parasite populations (Anderson and Gordon 1982; Wilber et al. 2017). In this respect, differences in parasite distributions with host age has received considerable attention (Anderson and Gordon 1982; Pacala and Dobson 1988).

The abundance and aggregation of some parasites steadily increase with host age, whereas other parasite species show peaks in younger host age classes (Krasnov et al. 2006; MacIntosh et al. 2010). Variation in aggregating and disaggregating mechanisms with host age drives the nature of this association. Whereas heterogeneity in susceptibility and exposure to parasites among host individuals generate aggregation (Poulin 2007b), density-dependent mechanisms may reduce aggregation. These include density dependent parasite mortality, parasite-induced host mortality, and acquired immunity, which dampen the abundance-age and aggregation-age relationships, with important implications for host and parasite population dynamics (Anderson and Gordon 1982; Pacala and Dobson 1988; Cattadori et al. 2005). Cross-sectional studies of abundance-age and aggregation-age relationships provide information over short time scales. Whether these relationships and their biological drivers are constant over time is largely unknown, although this information is crucial to understand long-term disease dynamics. The present paper addresses the interrelationship between host age, parasite abundance and parasite aggregation, and the temporal consistency of these associations using long-term data from a fish-nematode host-parasite association.

Ever since Crofton (1971) pointed out the ubiquity of parasite aggregation, several methods have been provided to measure this fundamental property of parasite populations (see e.g. (Wilson et al. 2002; Poulin 2007b; McVinish and Lester 2020). The parameter *k* from the negative binomial distribution and the variance-to-mean ratio of parasite abundance are two common aggregation measures that are used to model parasite population dynamics and infer density-dependent regulation (Anderson and May 1978; Anderson and Gordon 1982). However, these two measurements lack a clear biological interpretation regarding the distribution of parasites among hosts as they simply measure the departure from a Poisson distribution (McVinish and Lester 2020). Furthermore, both measures are sensitive to varying mean values (Poulin 2013; McVinish and Lester 2020). For instance, the variance is highly constrained by mean parasite abundance so that when pooling data from different host-parasite associations, ~87 % of the log(variance) is explained by log(mean) (Shaw and Dobson 1995; Poulin 2013). This log-log plot of variance against mean is known as Taylor's power law (Taylor 1961), and the slope of this linear regression, *b*, is commonly used as an index for aggregation (McVinish and Lester 2020). Higher values of *b* indicate steeper increases in variance with increases in the mean, interpreted as increased aggregation. Mean parasite abundance is thus central for structuring parasite aggregation. However, attempts to identify ecological phenomena that affect *b* directly, rather than indirectly through affecting the mean, have not been fruitful (Poulin 2013). Other methods for measuring aggregation might be more fruitful to understand the distribution of parasites among hosts, and the biological mechanisms that structure these distributions.

A pervasive problem in studying aggregation is the constraints imposed by the number of parasites *P* and hosts *H* in a sample (Wilber et al. 2017). For instance, Poulin (2013) found that sample size explained much of the residual variation in *b* (i.e., variation beyond the 87 % explained by the mean number of parasites). Feasible set theory is a proposed method to study variation in aggregation due to biological processes while controlling for statistical constraints inherent in the data (Johnson and Wilber 2017; Wilber et al. 2017). The method predicts the most likely shape of Taylor's power law given the constraints imposed by *P* and *H*, by randomly assigning parasites to hosts based on sample *P* and *H* in an iterative process. The residual variance between this feasible set and the observed values is then a measure of the aggregation that is not accounted for by *P* and *H*. Another recently proposed measure of aggregation is the Hoover index (McVinish and Lester 2020). A beneficial feature of this measure for aggregation compared to other indices (see McVinish and Lester 2020 for a discussion) is that it has a clear and simple biological interpretation as it quantifies the proportion (from 0 to 1) of parasites in a sample that needs to be redistributed among the hosts in order to produce a uniform distribution (McVinish and Lester 2020). It is however important to note that the Hoover index will decrease as the mean increases due to Taylor's power law (McVinish and Lester 2020). Here we used both these methods when studying the distribution of a metazoan parasite species in its final host population. We chose feasible set theory for its ability to tease apart aggregation beyond the constraints imposed by mean parasite abundance, and the Hoover index as it relates to classical measurements of aggregation but has a simpler interpretation and is more robust to measurement error and less affected by low mean values (McVinish and Lester 2020).

The present study addresses long-term dynamics in the abundance and aggregation of a long-lived parasitic nematode (*Cystidicola farionis*) infecting a size- and age-structured fish population (Arctic charr, *Salvelinus alpinus*). We examine factors structuring the parasite population in host individuals and at the host population level. Age is one of the most important parameters structuring animal populations (Iannelli and Milner 2017). Temporal changes in the age structure of a host population can influence parasite population and disease dynamics (Ben-Ami 2019), but few empirical studies address how temporal changes in host age affect the abundance and aggregation of parasites. Host age should be particularly important for parasitization of fish populations, as these typically are age- and size-structured (Ebenman and Persson 1988).

The study took place in subarctic lake Takvatn, northern Norway, as part of an ongoing long-term ecological monitoring programme conducted for more than 30 years (Amundsen et al. 2019). *Cystidicola farionis* uses Arctic charr as its only final host in the lake and the benthic amphipod *Gammarus lacustris* as its only intermediate host. Both the parasite and its fish host can live for more than 10 years, resulting in older hosts accumulating high infections (Black and Lankester 1981). We investigate age-abundance and age-aggregation relationships and their temporal stability and ecological drivers over a period spanning 32 years. Individual feeding specializations is an important source of parasite aggregation in Arctic charr (Knudsen et al. 2004), and we therefore addressed whether temporal changes in feeding affected parasite abundance and aggregation. We also included fish size in our analyses, since it is an important determinant of diet composition and consumption rates (Amundsen et al. 2007; Sánchez-Hernández et al. 2019), with strong effects on the abundance and composition of parasites (Henriksen et al. 2016; Prati et al. 2020b). We use the recently proposed method of feasible set theory to investigate aggregation beyond the constraints imposed by mean abundance and sample size. Furthermore, we compare this method to another recently proposed alternative, the Hoover index. We hypothesize that:

1. Host age, size and dietary choice affect parasite abundance at the individual and population level of the host.
2. Parasite aggregation is affected by mean parasite abundance and heterogeneity in host body size and feeding mode.
3. Temporal changes in host age structure affects parasite aggregation indirectly via mean parasite abundance.
4. Decomposing the host population into age classes reduces aggregation.

Materials and methods

Data collection

Arctic charr were collected from a 15 km^2 large lake, Takvatn, in northern Norway as part of a long-term sampling programme (see Amundsen et al., 2019), where the length (mm), weight (g), age (yrs), sex and gonad maturation of each fish are recorded. Brown trout (*Salmo trutta*) and 3-spined stickleback (*Gasterosteus aculeatus*) are also present in the lake, but they do not become infected with *Cystidicola farionis* (hereafter '*Cystidicola*'). Swimbladders from a total of 2871 charr were collected annually from 1987 until 2018 with the exception of years 1989, 1990, 1998, 1999 and 2007. These were stored in ethanol (96 %) from which the total number of nematodes are easily counted. All samples were collected in the ice-free period (June to November), with the exception of 1987, which also included monthly sampling during the winter. Because the seasonal variation of *Cystidicola* in the 1987 material was low (Knudsen and Klemetsen 1994), we included all sampling months to utilize the full material. Fish were collected from the littoral (< 15 m depth), pelagic (offshore, upper 0 – 6 m of the water column at > 30 m depth) and profundal (25 – 40 m) habitats of the lake.

Measuring heterogeneity in feeding

Arctic charr becomes infected with *Cystidicola* through a benthic feeding mode where fish individuals specialize on benthic invertebrates such as the amphipod intermediate host *G. lacustris*, and snails and insect larvae. High infections of *Cystidicola* is thus an indicator of a benthic feeding mode over time (Knudsen et al. 2014). Other Arctic charr individuals may specialize on feeding on pelagic crustaceans (zooplankton) or fish prey, and these rather accumulate high infections of the long-lived *Dibothriocephalus* spp. tapeworm larvae, as zooplankton (copepods) and small-sized fish are respective first intermediate and paratenic hosts of these tapeworms (Knudsen et al. 1996; Henriksen et al. 2016), but do not transmit *Cystidicola* (Knudsen et al. 2014). Stable isotope analyses in combination with stomach content data have shown that the number of *Dibothriocephalus* larvae is a reliable tracer of long-term dietary preferences towards these two prey types (Knudsen et al. 2014). We therefore used the number of *Dibothriocephalus* spp. tapeworms as a measure of a non-benthic feeding mode. When ingested, *Dibothriocephalus* larvae rapidly migrate from the stomach to the body cavity where the host encapsulate them in cysts (Halvorsen 1970). The total number of cysts is easily counted and provides a precise estimation of the total number of *Dibothriocephalus* larvae (Kuhn et al. 2017). When available in our long-term data set, we use cyst counts as our measure of *Dibothriocephalus* abundance, whereas in some years only the total number of larvae were counted and we then used the larval counts directly.

Data analyses

Parasite populations are nested at different levels of the host population (Bush et al. 1997). We analyzed parasite abundance at three levels; infrapopulation (at the individual host level), component population (average abundance across all hosts each year) and age class cohorts (age class within component populations). Because aggregation is a population level metric, it is necessarily only analyzed for component populations and age class cohorts. By analyzing abundance and aggregation at these respective levels, we try to tease apart effects that structure parasite aggregation directly, and indirectly through affecting parasite abundance.

Measuring aggregation

The Hoover index is calculated from:

$$\frac{\sum_{i=1}^{n}|x_i - \bar{x}|}{2n\bar{x}}$$

which is the sum of the absolute differences from the mean divided by twice the sum of the values. It ranges from 0 to 1 and takes the minimal value when all hosts have the same parasite burden and the maximal value when all parasites are concentrated in a single host (McVinish and Lester 2020). Additionally, we used the feasible set approach of Johnson & Wilber (2017) to measure the residual aggregation in Taylor's power law, beyond the constraints imposed by the total number of hosts, H, and parasites, P, in the sample (Fig 1B). This method randomly assigns parasites to hosts based on P and H. Due to the high number of parasites and hosts at the component population level, the analysis would not run due to lack of computational power. Therefore, we only use feasible set analysis for age class cohorts. For every age-class cohort, we extracted P and H and randomly sampled 1000 configurations from the feasible set. For each configuration, we calculated the $\log_{10}$ variance and used the median $\log_{10}$ variance across the 1000 configurations as the feasible set predicted log variance following Johnson & Wilber (2017). The difference between the observed and predicted log variance is thus the variance unaccounted for by P and H, constituting our measure of unexplained aggregation. For the lack of a better term, we call this measure the "feasible set aggregation". For all analyses at the age class level, we only included samples with > 2 hosts and > 3 parasites (Johnson & Wilber, 2017). Our final dataset for age class cohorts consisted of 175 host-parasite distributions with a total of 2664 hosts and 673845 parasites.

Infrapopulations

We first addressed how the predictor variables age, length, sex, and *Dibothriocephalus* larvae were related to *Cystidicola* abundance in individual fish (hypothesis 1). We included sex as a predictor variable because parasite infections in Arctic charr can differ between females and males (Skarstein et al. 2005). For analyzing *Cystidicola* abundance in fish individuals we applied a mixed-effect model with a negative binomial error distribution using the glmmTMB package (Brooks et al. 2017) in the R software (R Core Team, 2020). Host age (continuous variable) length (continuous), sex (factor) and number of *Dibothriocephalus* cysts (continuous, as a proxy for non-benthic feeding) were included as fixed effects, and year was included as a random effect. We included a random slope for age to test for differences in the relationship between parasite abundance and age among years. Fish that are born in the same year (i.e., belong to the same year class) should have experienced similar infection pressures throughout their life. We therefore added year class (year of birth = sampling year – age) as a crossed random effect. We also compared the model with a random slope for age with year to a model with random slope for age with year class to see if the parasite abundance~age slope (which can be thought of as a measure of infection pressure, McCallum et al. 2001) varied more with year class than with sampling year. We checked for non-significant dispersion in the model residuals using the R package DHARMa (Hartig 2020). We also inspected model residuals for autocorrelation. There was no need to include a term for zero-inflation as the model diagnostics indicated a proper fit, and overall prevalence was high (83% infected) and there are no false zeros in the data.

Component population

At the component population level (n = sampling years = 28), we calculated parasite mean abundance in each year. We then used multiple regression to predict mean abundance using mean age and length, sex (calculated as the proportion of males each year) and mean number of *Dibothriocephalus* as predictor variables (hypothesis 1). We used a similar regression approach as with mean abundance to predict the Hoover index. Here, we included *Cystidicola* mean abundance, heterogeneity in length and feeding mode as predictors of aggregation (hypothesis 2). To get a heterogeneity measure that is independent of the mean we regressed the $\log_{10}$ of variance against $\log_{10}$ of the mean for length and *Dibothriocephalus* respectively, and used the residuals of this regression as our predictor variable representing heterogeneity in body size and feeding mode. In addition to mean abundance, we also included *Cystidicola* prevalence (percentage of infected hosts) as a predictor of aggregation (Poulin 2007b). Although other potential predictors of aggregation could be included here, such as mean length, sex and feeding mode, we refrained from doing so due to the low number of observations (28) and the risk of overfitting models.

To address the direct and indirect effects of host age, feeding heterogeneity and heterogeneity in body size on parasite aggregation (hypothesis 3) we used piecewise structural equation modeling (SEM) (Lefcheck 2016). SEM is a form of path analysis that allows the simultaneous test of multiple relationships while controlling for potential correlations using a set of regression models that describe all hypothesized direct and indirect relationships in the data.

Age class cohorts

We split the data into age class cohorts to see how parasite abundance aggregation varied across specific host ages, and to see how decomposing the age structure affected our aggregation estimates (hypothesis 4). Here, we used both the Hoover index and feasible set aggregation as response variables. As predictors of aggregation across the age class data, we included mean fish length (i.e., average length at a specific age), heterogeneity in mean fish length (the residuals from regressing $\log_{10}$ variance length against $\log_{10}$ mean length), heterogeneity in *Dibothriocephalus*, and age as fixed effects, with year as a random effect in a linear mixed model. Heterogeneity in length within the age class cohorts corresponds to differences in the lifelong growth among fish. We included a random slope for age to test if the age-aggregation relationship changed over time. We used two separate models with the Hoover index and feasible set aggregation as respective response variables. Finally, we used SEM to infer direct and indirect relationships between host attributes, parasite abundance and parasite aggregation (hypothesis 3). Because of the higher number of observations at the age class level compared to the component population level (175 vs. 28), we could fit more complex models for age class cohorts.

Results

Infrapopulations

2387 out of 2871 Arctic charr were infected with *Cystidicola farionis* (Prevalence: 83 %, median abundance: 15, mean: 255, range: 0 – 7616). *Cystidicola* abundance increased with fish age and decreased with the number of *Dibothriocephalus* present (Table 1). Parasite infrapopulations were larger in male Arctic charr than in females. Our results indicated variation in the relationship between parasite abundance and fish age across years, as including a random slope for age with year significantly improved the model (ΔAIC 33, likelihood ratio test [LRT] $\chi = 36.584$, $P < 0.001$) compared to the model with only a random intercept. When including year class in the analyses the model residuals showed significant deviation. Excluding fish cohorts prior to 1986 (967 fish removed) resolved this issue. Including year class as a crossed random effect significantly improved the model (ΔAIC 36, LRT $\chi = 38.012$, $P < 0.001$, Table 2), indicating different intercepts among year classes. Further, the effect of host sex and *Dibothriocephalus* was no longer present (Table 2). Including a random slope for age with year class rather than sampling year did not improve the model (ΔAIC 11, LRT $\chi = 0$, $P = 1$). This indicates that variation in the abundance-age slope was of greater importance among sampling years than among year classes for the observed variation in *C. farionis* abundance, at least when cohorts prior to 1986 were excluded.

Individual Arctic charr age and length was highly correlated (Pearson's r = 0.84, df = 2869, $P < 0.001$). Replacing age with length in the mixed model in Table 1 resulted in significant deviation in model residuals, and we therefore present the age model here. The main difference between the two models was that the effect of host sex on parasite abundance was lower in the length model (see supplementary Table 1).

Component populations

At the component population level, the relationship between the variance and mean abundance among years closely followed Taylor's power law (Fig 1 A). There were yearly fluctuations in *Cystidicola* mean abundance (lowest: 5.0 in 2013, highest: 657.0 in 1992) with no temporal trend in the mean (Fig 2, supplementary Fig. 1). *Cystidicola* mean abundance increased with mean age and mean length (Fig 2). There were no clear effects of mean number of *Dibothriocephalus* larvae, heterogeneity in *Dibothriocephalus* larvae or sex ratio on parasite mean abundance (all $P > 0.10$). Annual variation in *C. farionis* aggregation, measured by the Hoover index, decreased with mean parasite abundance, and increased with heterogeneity in size with a weak positive effect of heterogeneity in *Dibothriocephalus* cysts (Table 3). Parasite mean abundance and prevalence were correlated (Pearson's $r = 0.55$, $df = 25$, $P = 0.003$). Replacing mean abundance with prevalence as a predictor variable, resulted in similar R^2 and AIC values, but the effects of fish size and *Dibothriocephalus* were less clear (P-values 0.13 and 0.08 respectively, supplementary Table 2).

Our SEM that age was the main predictor of parasite mean abundance, which in turn negatively affected aggregation. Heterogeneity in body size and feeding mode (number of *Dibothriocephalus* larvae) had direct and positive effects on aggregation with no effects on mean abundance. There was also an indirect effect of size heterogeneity through heterogeneity in feeding mode.

Age class cohorts

Within age class cohorts, mean abundance increased exponentially until age 10, with lower values for 11 and 12 year old age classes (Fig. 4A). The temporal variations in the abundance-age relationship indicated by the infrapopulation mixed model (Tables 1 and 2) largely followed changes in the size of specific age class cohorts (see supplementary Fig. 2).

Feasible set aggregation

Splitting the data by age within years reduced both the intercept (age class cohorts: 0.57 vs component population = 0.98) and slope, b, (age class cohorts: 1.81, component population: 1.89) of Taylor's power law (Fig. 1). For the feasible set, most age class cohorts were more aggregated than expected by P and H alone (Fig 1B). However, the observed and expected variation converged at higher mean abundances of *C. farionis*, and some age class cohorts were less aggregated than expected (Fig 1B).

There was a general decrease in feasible set aggregation with age (Fig 4B). Age and mean abundance were correlated (Pearson's r = 0.73, df = 173, $P < 0.001$), and could not be used as predictors in the same model. Parasite mean abundance explained more of the variation in feasible set aggregation than host age (Marginal $R^2 = 0.252$ vs. 0.227, ΔAIC 6.6, LRT $\chi = 0$, $P = 1$). An increase of 1 standard deviation in mean abundance reduced the difference between the observed and predicted variance by 0.18 (95 % CI: -0.13 - -0.23). The effect size was similar for age (-0.17, CI: -0.12 - -0.22). There was no effect of heterogeneity in fish size or *Dibothriocephalus* cysts on feasible set aggregation. We wanted to see if the patterns were consistent across years by including random slopes for mean abundance and age. The model with a random slope for mean abundance failed to converge. A random slope for age was not an improvement over the intercept only model (ΔAIC 2.1, LRT $\chi = 2$, $P = 0.39$), and the slope between aggregation and age was negative in all years. This indicates that the relationship between aggregation and age was fairly consistent (and negative) over the 31-year period. For the SEM, the tests of direct separation indicated that we could not separate between the direct effect of age on aggregation and the indirect effect via mean abundance (*P* = 0.01). Replacing age with length resolved this issue. The SEM indicated that mean abundance and prevalence had direct negative effects on feasible set aggregation (Fig 5). Mean fish size had indirect negative effects on aggregation by increasing *C. farionis* mean abundance and prevalence. Mean number of *Dibothriocephalus* cysts (i.e., proxy for feeding in the water column) had indirect positive effects on aggregation through reducing *C. farionis* mean abundance. There were no direct effects of heterogeneity or mean feeding mode on feasible set aggregation among age class cohorts (Fig 5).

Hoover index

The Hoover index correlated positively with the residual aggregation from the feasible set (r = 0.92, df = 173, $P < 0.001$; supplementary Fig. 3). Accordingly, models predicting Hoover index were similar to those predicting feasible set aggregation. Hoover index decreased with mean abundance and age with weak positive effects of heterogeneity in size and feeding (supplementary tables 3 and 4). Once again, the models with mean abundance performed better than with age as predictor (ΔAIC 15.7, LRT χ = 15.6, $P < 0.001$). The SEM for the Hoover index was very similar to the SEM for feasible set aggregation**,** the main difference being that heterogeneity in size had a positive effect on the Hoover index (supplementary Fig. 4)

Discussion

Despite the vast literature on parasite aggregation, few studies have been able to study long-term patterns in parasite abundance and aggregation. In the present study, we tracked changes in the abundance and aggregation of a long-lived nematode parasite over three decades. Changes in the age- and size-structure of the host population accounted for around half the variation in mean parasite abundance. Parasite aggregation decreased as parasite abundance increased, indicating more homogenous parasite populations in years when large, old and highly parasitized fish dominated the population. Hence, there was an indirect negative effect of host age on parasite aggregation, and this relationship was stable over the study period. At the component population level, heterogeneity in host body size and feeding mode increased aggregation. However, splitting the data into age class cohorts largely canceled out these effects, pointing to the importance of accounting for host age structure when attempting to identify mechanisms that structure parasite populations.

The most important predictors of nematode abundance in fish individuals were age and size. It is difficult to tease apart the relative contribution of host age and size to the observed infection patterns, as the two are highly correlated. Larger fish offer more habitat for parasites, need more energy and their elevated consumption rates increase their exposure to potential intermediate hosts (Cardon et al. 2011; Henriksen et al. 2019b). Furthermore, larger fish are older and accumulate more parasites over time. This accumulation over time is mostly relevant for parasites that are long lived (Zelmer and Arai 1998), which is the case for the studied *Cystidicola* nematode that can survive in the swimbladder for the lifespan of the host (Black and Lankester 1981). Fish size affects dietary choice (Sánchez-Hernández et al. 2019), and individual dietary specializations was important for *Cystidicola* abundance in Arctic charr. Fish that had higher infections of *Dibothriocephalus* tapeworms, transmitted via pelagic copepods and thus used as a proxy for a more pelagic feeding mode, had lower infections of *Cystidicola* that are transmitted via benthic amphipods.

At the component population level, mean parasite abundance fluctuated at the beginning of the times series, but there was no temporal trend and oscillations decreased in the last half of the study period. Mean age and length of the host population explained roughly half of the variation in parasite mean abundance among years. Because parasite abundance in fish individuals varied from zero to more than 7000 parasites, mean values are sensitive to outliers that might be sampled in one year but not the next. Median abundance, on the other hand, captures the central tendency of infection levels in the average host individual. Interestingly, median abundance increased exponentially with host size (supplementary Fig. 4). The median abundance was below 50 in 23 out of 27 years. The only years in which median abundance was above 50 were the four years where average fish length was above 25 cm. This length corresponds to the size when Arctic charr in Takvatn shift their diet away from zooplankton (25.3 cm) and towards benthic prey (24.8 cm, P-A Amundsen, unpublished data), resulting in a dramatic change in the exposure to trophically transmitted parasites (Prati et al. 2020b). Ontogenetic dietary shifts are typically related to the size of an organism (Werner and Gilliam 1984; Sánchez-Hernández et al. 2019). For trophically transmitted parasites that infect size-structured populations, shifts in the size-structure of the host population will therefore have strong impacts on the parasite population. The size-distribution and ontogenetic dietary shifts of Arctic charr have been relatively stable over the last 20 years in Takvatn (Prati et al. 2021). This, in combination with the long life-span of *Cystidicola farionis* are probably important for the fairly stable situation we observe in the present time-series study.

Despite the lack of a trend in parasite mean abundance over time, age-abundance curves varied among years suggesting that the infection pressure changed over the three-decade study period. In particular, fish born earlier than 1986 had lower infections of *Cystidicola* than the later cohorts did. This has been noted in previous studies from Takvatn as well (Knudsen et al. 1999, 2002). In the early 1980s, the Arctic charr population was overcrowded and dominated by old, slow-growing fish that predominantly fed on zooplankton, with large benthic prey items being nearly depleted (Amundsen and Klemetsen 1988). The whole-lake fish culling experiment that removed more than 30 tons of Arctic charr between 1984 and 1989 resulted in a new stable state with fast-growing fish that fed mostly on benthic invertebrates as adults (Klemetsen et al. 2002; Persson et al. 2007; Amundsen et al. 2019). Although the fish culling reduced the infections of *Dibothriocephalus* tapeworms, it probably facilitated the transmission of *C. farionis* through increasing the abundance of and consumption on amphipods (Knudsen et al. 1999; Henriksen et al. 2019a, present study). The new stable state is reflected in the stable high infections of *Cystidicola* that we observed in the last two decades of the present study. Paradoxically, reducing host density increased the transmission of *Cystidicola* through elevated consumption rates towards the intermediate hosts and larger host body sizes. We did not include stomach content data from the fish in the present study. The reason for this is that Arctic charr in Takvatn feed mainly on insects and zooplankton during the ice-free period (when sampling is conducted), whereas the feeding on amphipods and transmission of their parasites predominantly occur under the ice during winter (Prati et al. 2020a). However, the degree of individual dietary specializations has changed over time in Arctic charr due to changes in the density of the competitor and predator, brown trout (Prati et al. 2021). The fact that infection pressures differed more among sampling years than among year classes suggests that it is probably the degree of individual dietary specialization from year-to-year, rather than the cumulative exposure of a single age class to parasitic stages, that is important for the long-term fluctuations in the abundance-age relationship in the post-culling period.

As expected, the relationship between the mean and variance of parasite abundance closely followed Taylor’s power law (TPL). The tight fit of parasite distributions to TPL suggests that the degree of parasite aggregation is constrained for a given mean abundance (Shaw and Dobson 1995; Poulin 2007b). In the present study, the distribution of parasites became more uniform (i.e. aggregation decreased) with increasing parasite prevalence and abundance, a relationship documented across several host-parasite systems (Poulin 1993, 2007b). Accordingly, temporal changes in parasite aggregation largely followed changes in parasite prevalence and abundance, which, in turn, was determined by host size and age. This held true for feasible set aggregation among age class cohorts as well, which accounts for the number of hosts and parasites in the sample. The two measures we used for aggregation, the Hoover index (McVinish and Lester 2020) and a method based on feasible set theory that accounts for statistical constraints in the data (Johnson and Wilber 2017) showed a high degree of correlation. This was reassuring, but partly also surprising as the former is a simple measure of departure from a uniform distribution, whereas the latter is a statistical procedure to account for aggregation beyond the constraints imposed by the number of hosts and parasites in the sample. The reduced parasite aggregation at higher infection levels suggests that regulatory processes such as parasite mortality, parasite-induced host mortality or immunity are operating (Anderson and Gordon 1982; Cattadori et al. 2005). It is difficult to infer which mechanism constrains parasite aggregation from field data alone (Wilber et al. 2017). A simple explanation could simply be a lack of space for the establishment of new parasites in heavily infested swimbladders. Knudsen et al. (2002) suggested that parasite-induced host mortality was the most plausible explanation for observed distributions of *Cystidicola* in Arctic charr since they seldom observed dead nematodes in the swim bladder. This is certainly possible, however, increased host resistance due to repeated exposure resulting in reduced parasite establishment rates is also a possibility (e.g. Stables and Chappell 1986; Höglund and Thuvander 1990). If parasite-induced host mortality is operating this would ensure that the largest charr, which achieve the highest parasite burdens, are removed from the population. This would facilitate regulation and stability in the host-parasite system (Anderson and May 1978; Knudsen et al. 2002) . It is worth noting that in nearby lakes where *Cystidicola* is not present but Arctic charr still feed on *Gammarus*, charr achieve much larger sizes than in Takvatn and adjacent Fjellfrösvatn where the parasite is present (Henriksen et al. 2019b, unpublished data).

Heterogeneity in fish size increased parasite aggregation at the component population level as hypothesized. The effects were both direct and indirect through effects on heterogeneity in feeding mode. This is in line with previous work showing that heterogeneity in host size and diet facilitate parasite aggregation (Poulin 2007b; Johnson and Hoverman 2014). As heterogeneity in size and age were highly correlated (Pearson's r = 0.80), it is difficult to tease apart the effects of heterogeneity in size and age on aggregation. However, as size is the most important predictor of diet in Arctic charr (Klemetsen et al. 2003), a population consisting of fish of several size (and thus age) groups will feed on variable prey types thereby generating aggregated distributions of trophically transmitted parasites. In fish populations dominated by a few strong year classes, the variation in sizes will be limited and aggregation will likely decrease. When we split the data into age class cohorts, the effect of heterogeneity in size on parasite aggregation almost disappeared. Among age class cohorts, parasite abundance and prevalence had the strongest effect on aggregation, which in turn were predicted by body size and age. However, although it might be expected that infections within a single age class would remain temporally stable, parasite abundance displayed considerable variation over time, also within ages. This was chiefly linked to differences in growth (size at age). For instance, 6-year old Arctic charr have increased in size from the mid 2000s towards the end of the study, which corresponded to an increase in the mean and median abundance of *Cystidicola* (supplementary Fig 2).

In a 23-year study on five helminth parasites of European rabbits, Boag et al. (2001) observed considerable variation in aggregation among years. Host age affected the aggregation of all parasite species, but to a varying degree, and they concluded that aggregation was a temporally dynamic and variable process (Boag et al. 2001). Our results also show that there is a high degree of stochasticity in the temporal dynamics of aggregation, as more than half of the variation in aggregation could not be accounted for by any of our predictor variables. Nonetheless, we found clear evidence that temporal variation in parasite abundance and prevalence set the boundaries for aggregation, and that temporal changes in parasite abundance are governed by the age and size structure of the host population. The importance of acknowledging that host age structure varies across time, and that this has important epidemiological and ecological implications has recently been highlighted (Ben-Ami 2019). In Takvatn, the size- and age distribution and ontogenetic dietary shifts of Arctic charr has shifted over time due to intraspecific competition as well as interspecific competition with and predation from brown trout (Klemetsen et al. 2002; Persson et al. 2007; Amundsen et al. 2019). The long-term nature of these size-structured interactions (Ebenman and Persson 1988) appear to be the most important determinant of long-term change in the transmission of trophically transmitted parasites to Arctic charr in the lake (Henriksen et al. 2019a, present study).

The slope of *b* from Taylor's power law is around 1.5 for most host-parasite systems and rarely exceeds 2 (Shaw and Dobson 1995; McVinish and Lester 2020). In this respect, the aggregation of *Cystidicola* observed in the present study is high. Aggregation is predicted to stabilize the dynamic behaviour of host-parasite interactions and enhance the regulatory role of the parasite (Anderson and May 1978). It is therefore possible that the stability in the host-parasite dynamics we observed (supplementary Fig 1), can be attributed to density-dependent regulation of the host and parasite populations. However, we cannot rule out that the stable infection patterns over the last 20 years simply reflect stable abiotic and biotic conditions in the ecosystem (Kennedy 2009).

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Tables

Table 1. Results from generalized linear mixed effects model with negative binomial errors predicting *Cystidicola farionis* abundance in individual Arctic charr from Takvatn. Age (random intercept and slope), sex and number of *Dibothriocephalus* tapeworms (random intercepts only) are fixed effects with sampling year as a random effect.

	***Cystidicola farionis* abundance**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	46.23	32.51 – 65.74	**<0.001**
Age	8.22	6.71 – 10.07	**<0.001**
Sex [Male]	1.29	1.14 – 1.45	**<0.001**
Dibothriocephalus plerocercoids	0.90	0.83 – 0.97	**0.005**
Random Effects			
σ^2	1.24		
$\tau_{00\ \mathrm{Year}}$	0.79		
$\tau_{11\ \mathrm{Year.Age}}$	0.19		
$\rho_{01\ \mathrm{Year}}$	-0.21		
ICC	0.44		
N_{Year}	27		
Observations	2871		
Marginal R^2 / Conditional R^2	0.664 / 0.812		

Table 2. Results from generalized linear mixed effects model with negative binomial errors predicting *Cystidicola farionis* abundance in Takvatn. Age (random intercept and slope), sex and number of *Dibothriocephalus* tapeworms (random intercepts only) are fixed effects with sampling year and year class as random effects. The analysis excludes fish born earlier than 1986.

	***Cystidicola farionis* abundance**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	25.49	17.47 – 37.21	**<0.001**
Age	6.03	4.97 – 7.31	**<0.001**
Sex [Male]	1.14	0.97 – 1.34	0.109
Dibothriocephalus plerocercoids	1.07	0.97 – 1.19	0.183
Random Effects			
σ^2	1.29		
$\tau_{00\ \text{Year}}$	0.69		
$\tau_{00\ \text{Year class}}$	0.21		
$\tau_{11\ \text{Year.Age}}$	0.14		
$\rho_{01\ \text{Year}}$	-0.68		
ICC	0.45		
N_{Year}	27		
$N_{\text{Year class}}$	31		
Observations	1904		
Marginal R^2 / Conditional R^2	0.591 / 0.773		

Table 3. Summary statistics from multiple regression predicting the Hoover index each year, with scaled predictor variables and 95 % confidence intervals.

	Hoover index		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.67	0.64 – 0.70	**<0.001**
C. farionis mean abundance	-0.04	-0.07 – -0.01	**0.012**
Heterogeneity in body size	0.04	0.01 – 0.08	**0.014**
Heterogeneity in *Dibothriocephalus*	0.03	0.00 – 0.07	**0.043**
Observations	27		
R^2 / R^2 adjusted	0.470 / 0.401		

Figures

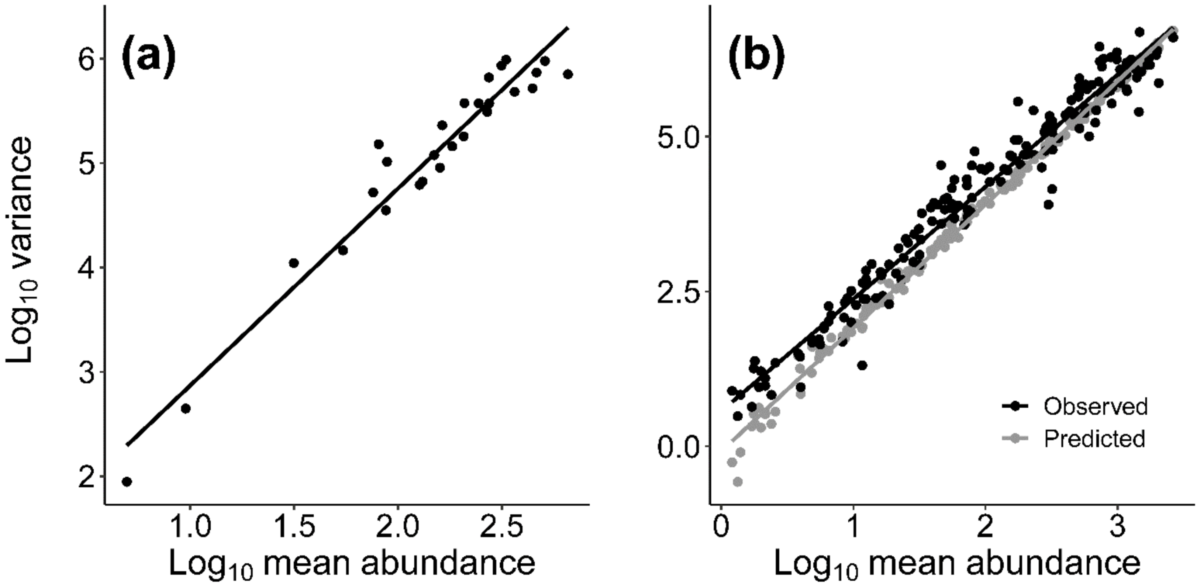


Fig 1. Slope of Taylor’s power law. (a) The observed relationship between log mean and log variance for the component populations in each year (n = 28). (b) The relationship between log mean abundance and log variance predicted from the feasible set (grey points) and the observed values (black points). Each point represents a specific age class cohort within a year (n =175).

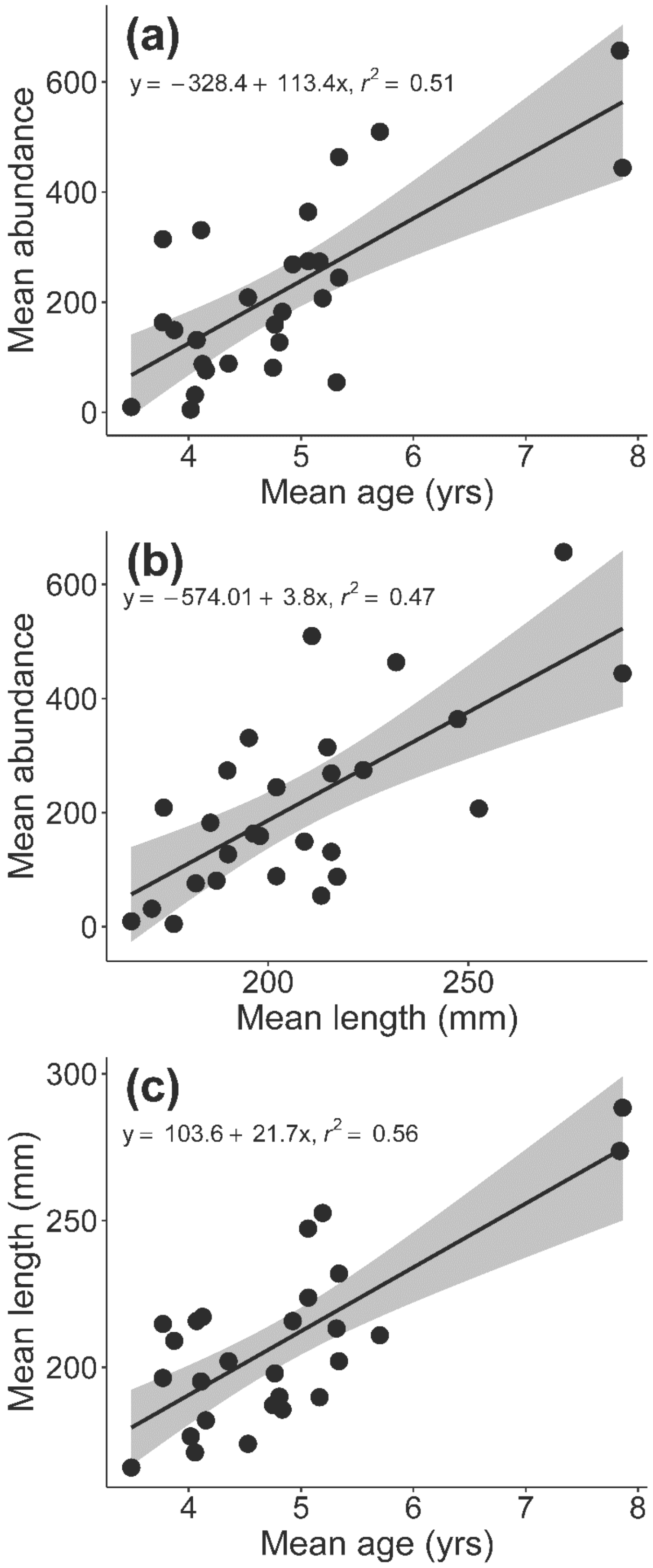


Fig 2. The relationship between the mean abundance of *C. farionis* and Arctic charr length (a), age (b) and the relationship between mean length and age (c).

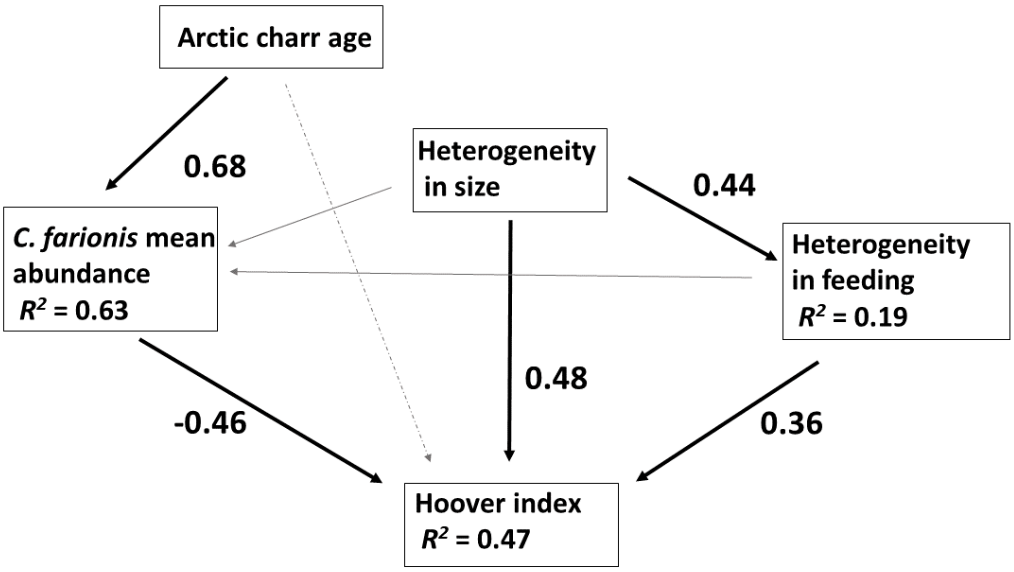


Fig 3. Structural equation model showing the relationships between Arctic charr age, heterogeneity in size, heterogeneity in feeding (*Dibothriocephalus* cysts) and *Cystidicola farionis* mean abundance and aggregation (measured as the Hoover index) at the component population level. Solid black arrows indicate significant relationships and thin grey arrows non-significant ones. Numbers in boxes denote standardized path coefficients from the structural equation model. R^2 values for the endogenous variables are shown. The tests of directed separation (stipled grey line) was not significant (P = 0.246) indicating no direct effect of age on aggregation.

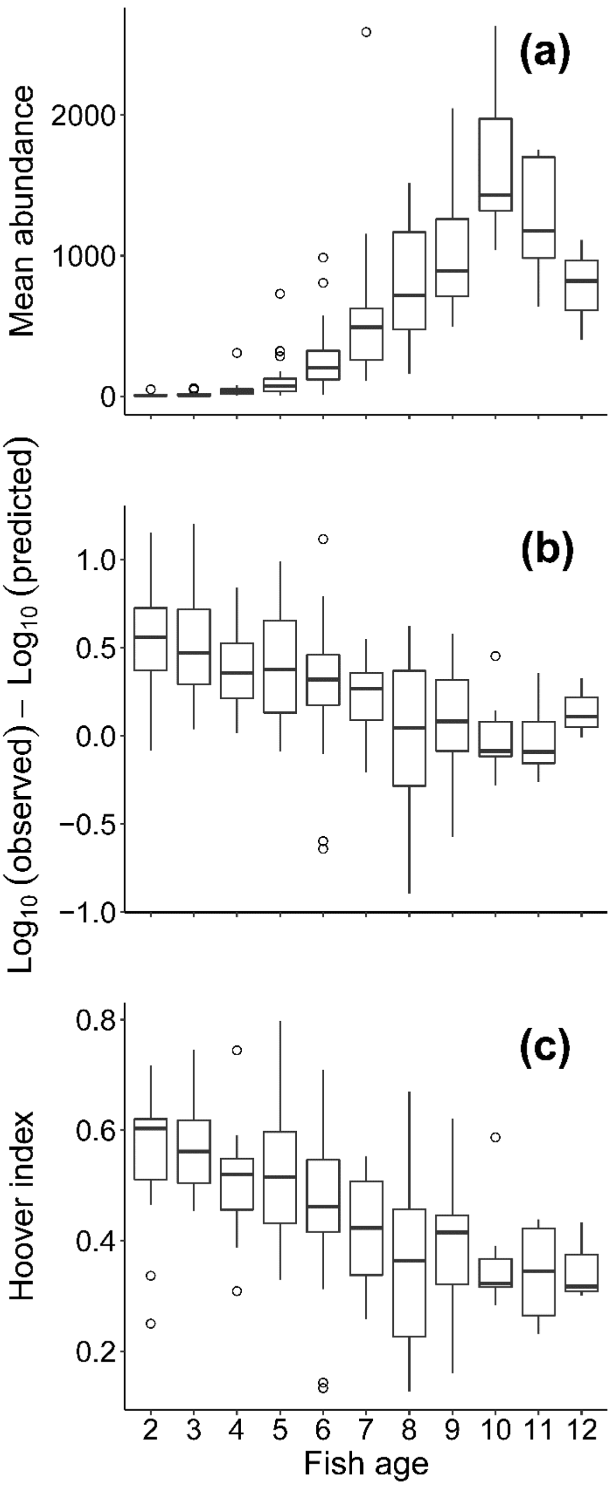


Fig 4. Boxplots showing (a) mean abundance of *Cystidicola farionis* calculated for age class chorts, i.e. a for each age within all years. (b) The difference between the observed and predicted $\log_{10}$ variance (i.e. feasible set aggregation, see fig 1b) and (c) the Hoover index among ages. Age class cohorts with only one observation (ages 1, 13, 14 and 15) are not shown.

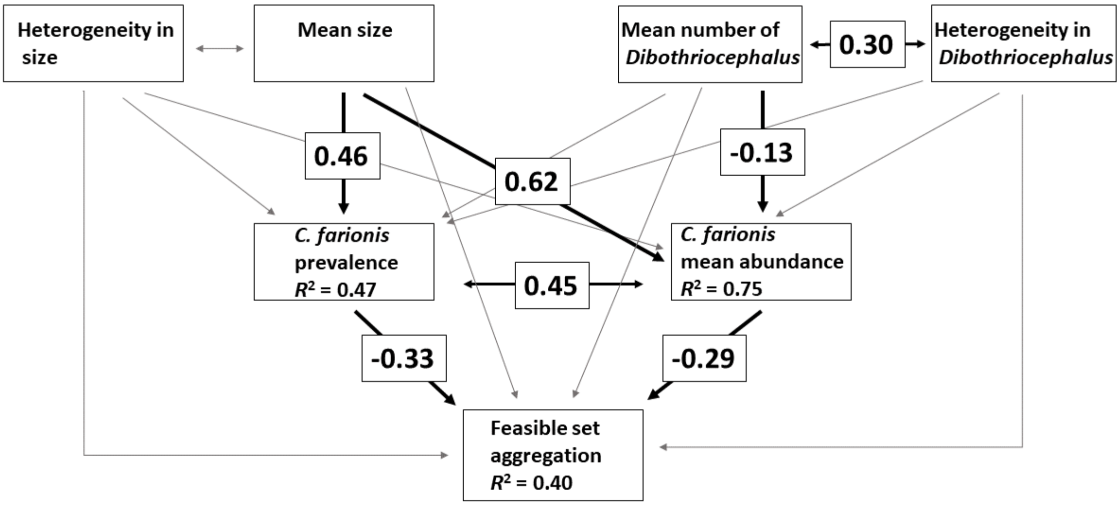
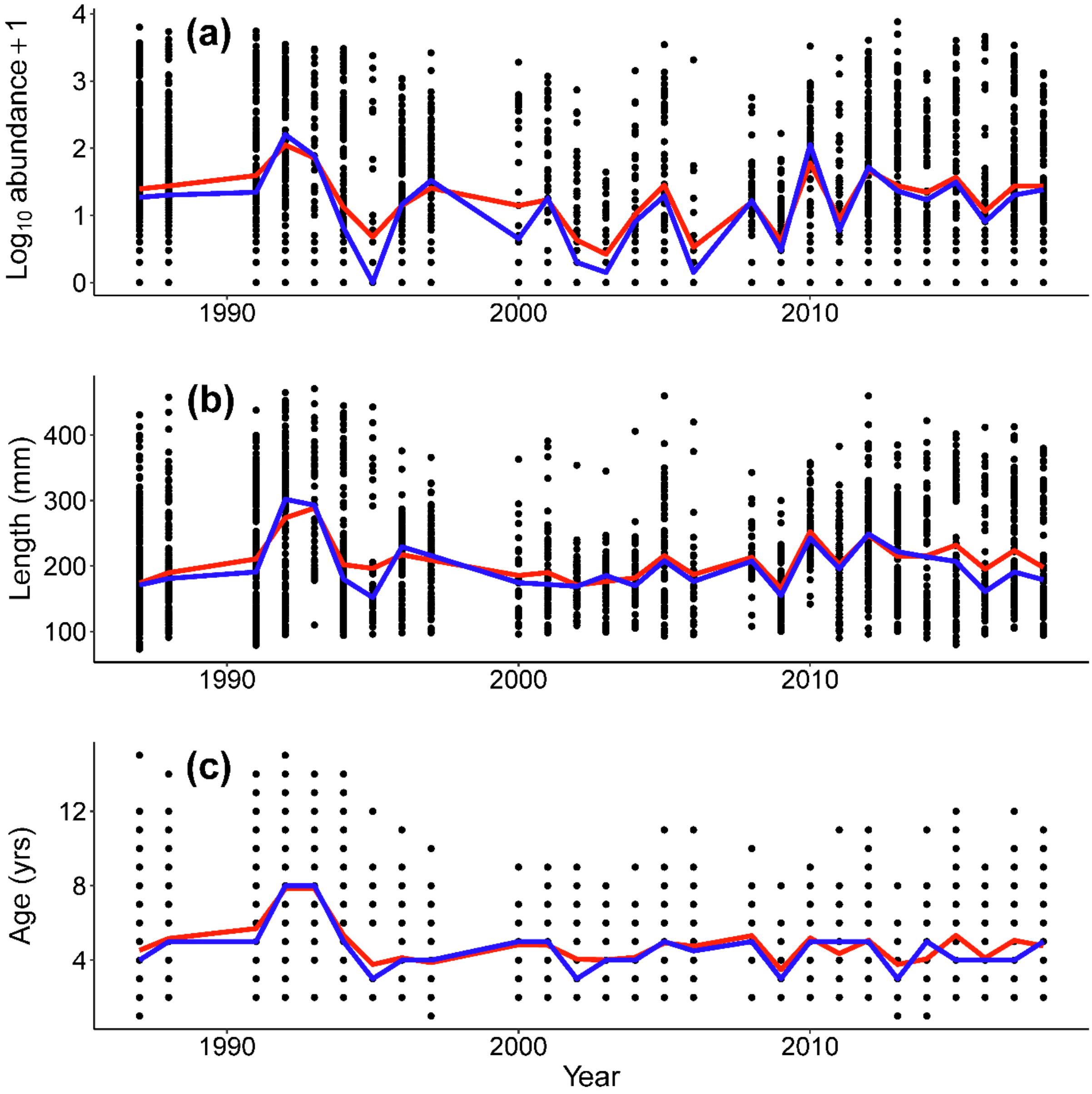
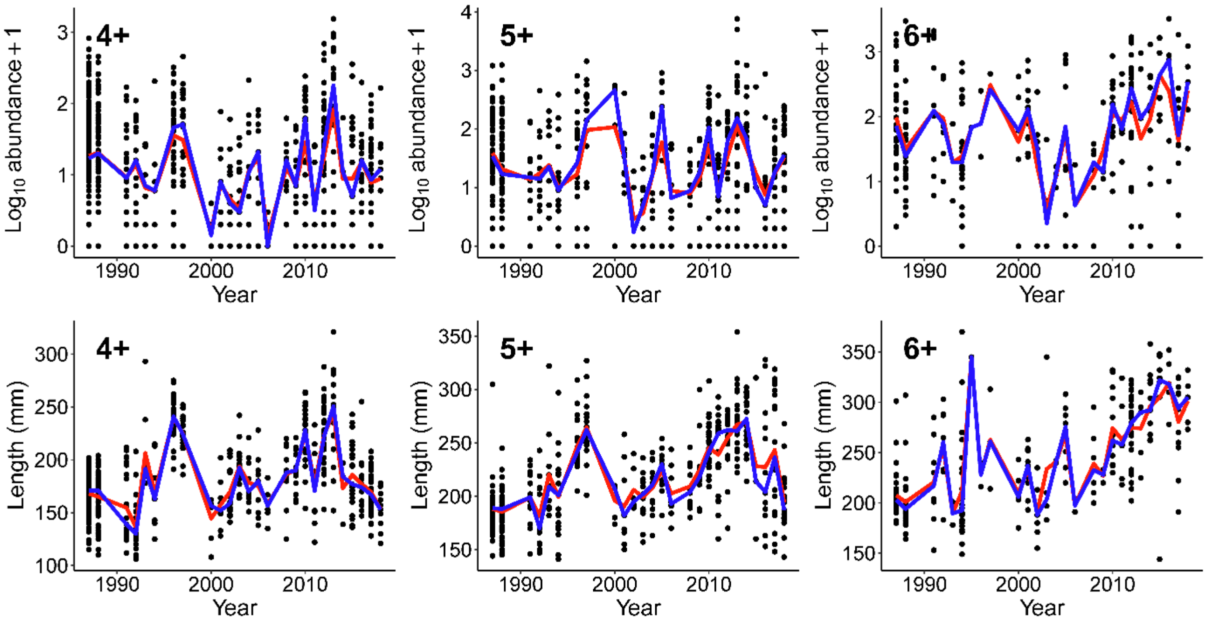


Fig. 5. Structural equation model showing the relationships between various predictor variables and *Cystidicola farionis* mean abundance, prevalence and aggregation (measured as feasible set aggregation) at the age-class cohort level. Solid black arrows indicate significant relationships and grey thin arrows non-significant ones. Solid black double-headed arrows indicate significant correlations, thin grey double headed arrows non-significant correlations. The numbers in boxes denote significant standardized path coefficients from the structural equation model, and Pearson's *r* for correlations. R^2 values for the endogenous variables are shown. Thin grey lines denote non-significant relationships. Year and age are included as random effects.

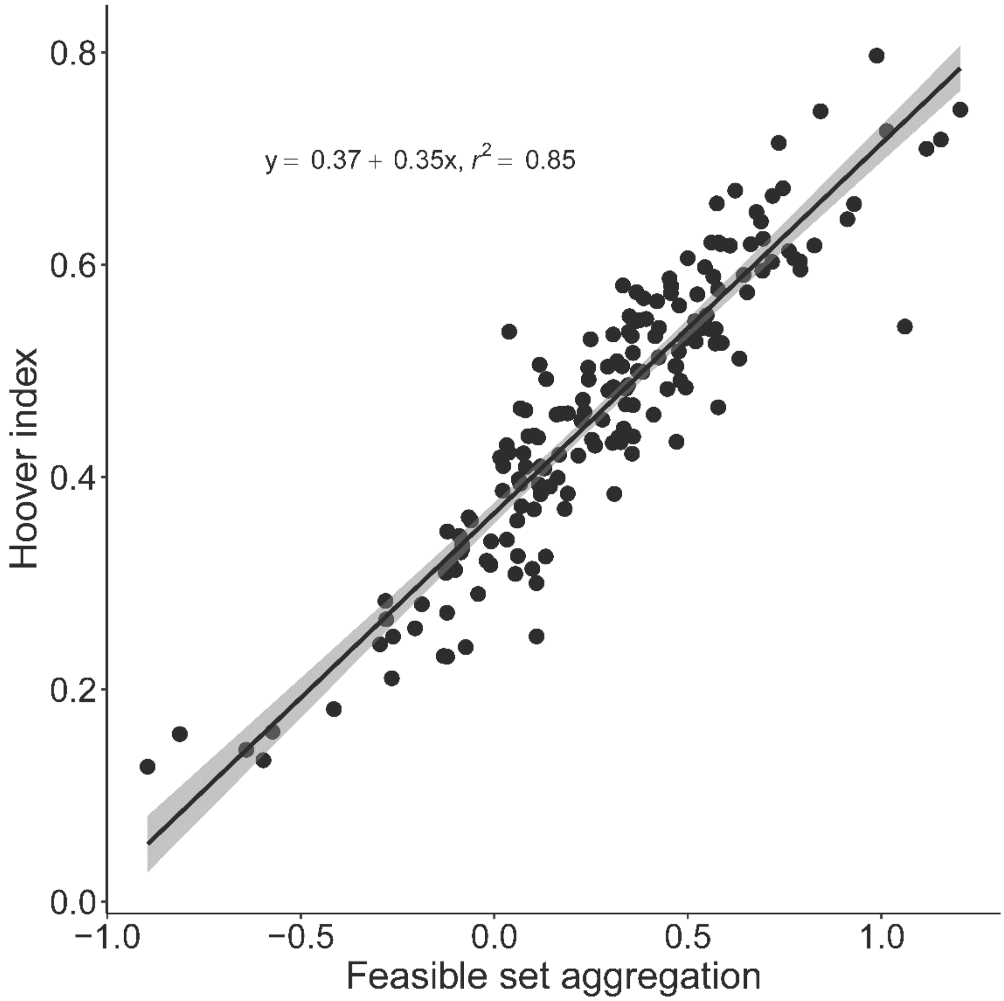
Supplementary information



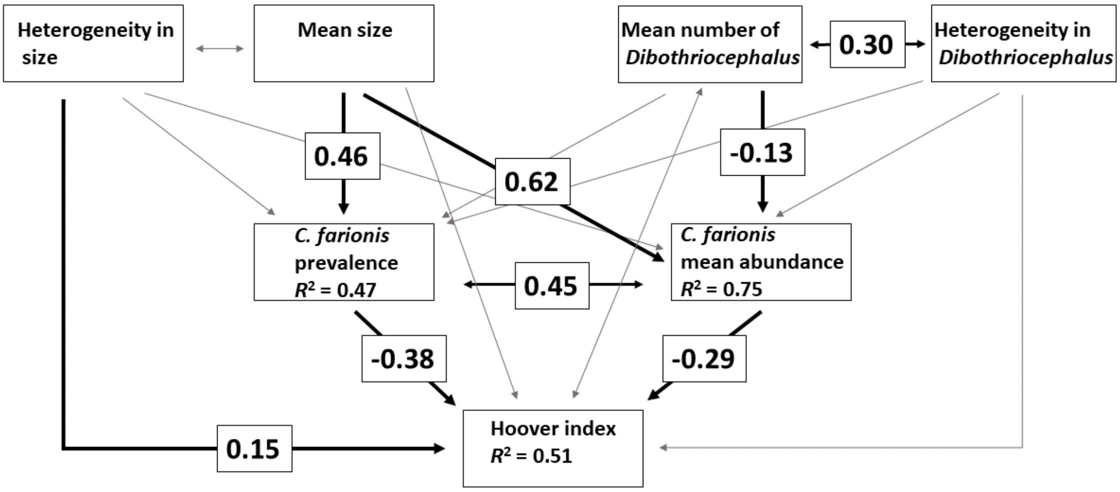
Supplementary fig 1. (a) Abundance (log10 + 1 transformation) of *Cystidicola farionis*, (b) length and (c) age of Arctic charr sampled between 1987 and 2018. Points represents individual fish. The red line indicates mean values and the blue line indicates the median.



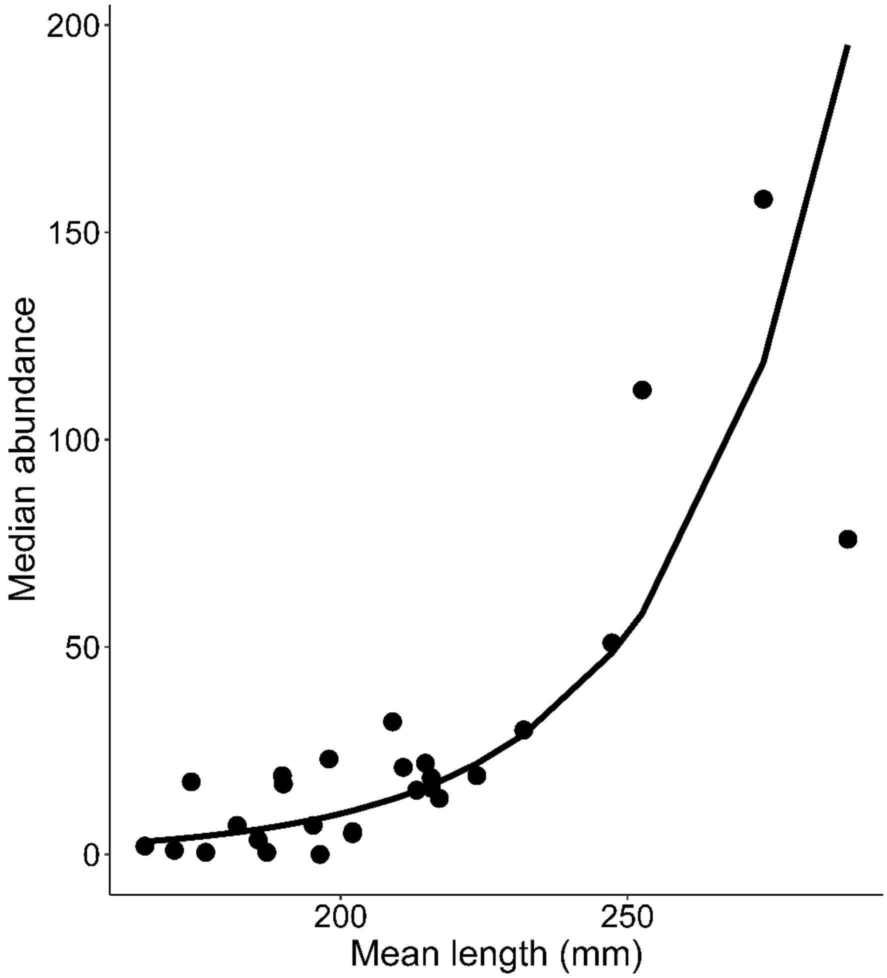
Supplementary fig 2. Abundance (log10 + 1 transformation) of *Cystidicola farionis* and length of 4-year old (left), 5-year old (middle) and 6-year old (right) Arctic charr in Takvatn sampled between 1987 and 2018. The red line indicates mean values and the blue line indicates the median. Points are individual fish.



Supplementary fig 3. The association between the Hoover index and feasible set aggregation for age class cohorts.



Supplementary fig 4. Structural equation model showing the relationships between various predictor variables and *Cystidicola farionis* mean abundance, prevalence and aggregation (measured as the Hoover index) at the age-class cohort level. Solid black arrows indicate significant relationships and grey thin arrows non-significant ones. Solid black double-headed arrows indicate significant correlations, thin grey double headed arrows non-significant correlations. The numbers in boxes denote significant standardized path coefficients from the structural equation model, and Pearson's *r* for correlations. R^2 values for the endogenous variables are shown. Thin grey lines denote non-significant relationships. Year and age are included as random effects.



Supplementary fig 5. The relationship between mean length of Arctic charr and the median abundance of *C. farionis*. The regression line is transformed from a linear regression of the form log (median abundance +1) ~ mean length: y = -4.47 + 0.03x, R^2 = 0.60. Each point represents a component population, i.e. sampling year.

Supplementary table 1. Results from generalized linear mixed effects model with negative binomial errors predicting *Cystidicola farionis* abundance in individual Arctic charr from Takvatn. Length (random intercept and slope), sex and number of *Dibothriocephalus* tapeworms (random intercepts only) are fixed effects with sampling year as a random effect.

	***Cystidicola farionis* abundance**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	46.92	34.89 – 63.10	**<0.001**
Length	7.42	6.11 – 9.02	**<0.001**
Sex [Male]	1.07	0.95 – 1.21	0.246
Dibothriocephalus plerocercoids	0.85	0.79 – 0.92	**<0.001**
Random Effects			
σ^2	1.23		
τ_{00} Year	0.54		
τ_{11} Year.scale(Length)	0.18		
ρ_{01} Year	-0.24		
ICC	0.37		
N Year	27		
Observations	2871		
Marginal R^2 / Conditional R^2	0.665 / 0.788		

Supplementary table 2. Summary statistics from multiple regression predicting the Hoover index each year, with scaled predictor variables and 95 % confidence intervals. Here, parasite prevalence, rather than mean abundance, is included as a predictor variable.

	Hoover index		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.67	0.64 – 0.70	**<0.001**
C. farionis prevalence	-0.04	-0.07 – -0.01	**0.011**
Heterogeneity in body size	0.02	-0.01 – 0.06	0.130
Heterogeneity in *Dibothriocephalus*	0.03	-0.00 – 0.06	0.083
Observations	27		
R^2 / R^2 adjusted	0.471 / 0.402		

Supplementary table 3. Results from linear mixed effects model predicting the Hoover index for age class cohorts in Arctic charr from Takvatn. Age, heterogeneity in *Dibothriocephalus* and heterogeneity in body size are fixed effects with sampling year as a random effect.

	Hoover index		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.46	0.44 – 0.49	**<0.001**
Age	-0.07	-0.09 – -0.05	**<0.001**
Heterogeneity in *Dibothriocephalus*	0.01	-0.01 – 0.03	0.288
Heterogeneity in fish length	0.02	0.00 – 0.04	**0.019**
Random Effects			
σ^2	0.01		
$\tau_{00\ \mathrm{AR}}$	0.00		
ICC	0.10		
N_{AR}	27		
Observations	175		
Marginal R^2 / Conditional R^2	0.308 / 0.376		

Supplementary table 4. Results from linear mixed effects model predicting the Hoover index for age class cohorts in Arctic charr from Takvatn. *Cystidicola farionis* mean abundance, heterogeneity in *Dibothriocephalus* and heterogeneity in body size are fixed effects with sampling year as a random effect.

	Hoover index		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.46	0.44 – 0.49	**<0.001**
C. farionis mean abundance	-0.07	-0.09 – -0.06	**<0.001**
Heterogeneity in *Dibothriocephalus*	0.02	-0.00 – 0.03	0.075
Heterogeneity in fish length	0.02	-0.00 – 0.03	0.064
Random Effects			
σ^2	0.01		
$\tau_{00\ AR}$	0.00		
ICC	0.13		
N $_{AR}$	27		
Observations	175		
Marginal R^2 / Conditional R^2	0.313 / 0.400