

## Research article

# Ectoparasites population dynamics are affected by host body size but not host density or water temperature in a 32-year long time series

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Host density, host body size and ambient temperature have all been positively 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. Negative intraguild interactions between brown trout and Arctic charr appear to drive smaller Arctic charr to seek refuge in deeper areas of the lake, thus 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 research and management. 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.

Keywords: Arctic charr, gill lice, host density, *Salmincola edwardsii*, *Salvelinus alpinus*

## Introduction

Understanding the biotic and abiotic drivers of population abundance is a central goal in ecology. Long-term ecological studies are essential to explain how and why populations respond to environmental change and management and conservation efforts



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(Lindenmayer et al. 2012, Kuebbing et al. 2018). Climate change affects the abundance and distribution of free-living species, and we need to address how parasites respond to these changes (Altizer et al. 2013, Byers 2021). For parasite populations, long-term studies are rare due to the time and cost required to sample hosts and screen them for parasites. This is unfortunate since temporal studies provide new insights into ecological patterns that cannot be observed on short time scales (Kennedy 2009, Hampton et al. 2019). Several biological and anthropogenic factors affect parasite population dynamics (Wood et al. 2010, Kołodziej-Sobocińska 2019). When multiple factors (e.g. harvesting, host body size, host density, host diversity, temperature) simultaneously vary through time it becomes difficult to realistically model the outcome for parasites. In this regard, time series can help address the direct and indirect effects of different abiotic and biotic factors on parasites and untangle their relative effects on parasite population dynamics.

Perhaps the most important long-term determinant of parasite abundance is host density. A central assumption of most host–parasite models is that parasite transmission increases with the density of hosts (May and Anderson 1979, Hopkins et al. 2020). Spatial studies and meta-analyses support this association for many 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 often 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 (Laguerre and Poulin 2015, Buck and Lutterschmidt 2017). Altogether, host density should regulate populations of directly transmitted parasites.

Besides host density, another intrinsic property of the host that affects both exposure and susceptibility to parasites is host body size. Larger hosts provide more space for parasite individuals (Poulin 2000). Further, host size correlates with host age, and larger hosts can therefore accumulate more parasites over time (Zelmer and Arai 1998). The processes that regulate the total number of parasites in a population operate at both the infrapopulation (parasites on an individual host) 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, changes in 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).

There is increasing concern as to how anthropogenic activities such as climate change, fishing and species introductions affect fish parasites (Wood et al. 2010, Goedknecht et al. 2016), and in particular ectoparasitic copepods on fish (Godwin et al. 2021). 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 *Salmincola*) 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. 1990b, 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 (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 effects if aggregation increases mating probabilities and does not induce host mortality (Krkošek et al. 2012, Cox et al. 2017).

Ecosystem perturbations combined with long-term monitoring provide excellent opportunities for addressing temporal drivers of parasite abundance (Kennedy 2009, Henriksen et al. 2019). In the present study, we utilize a unique long-term dataset spanning 32 years to investigate how fish density, body 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 if copepodids attempt to attach to brown trout but fail, thus expending their finite energy reserves. 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). We hypothesize that 1) fish size positively affects gill lice abundance at individual and population levels, and 2) parasite abundance and transmission rate increase with host density and temperature, but decrease with brown trout density. 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.

## Material and methods

### Study site

Takvatn (69°07'N, 19°05'E) is a 15 km<sup>2</sup> 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 m 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*. Brown trout is the only native fish species. Arctic charr and three-spined stickleback were introduced to the lake in 1930 and 1950, respectively (Amundsen et al. 2019). Of the three fish species, Arctic charr is the only suitable host for the parasitic copepod *Salmincola edwardsii*, and the parasite was introduced to the lake along with its host (Amundsen et al. 2013). 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). One main goal of the culling was to increase the somatic growth rates of both brown trout and Arctic charr. 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

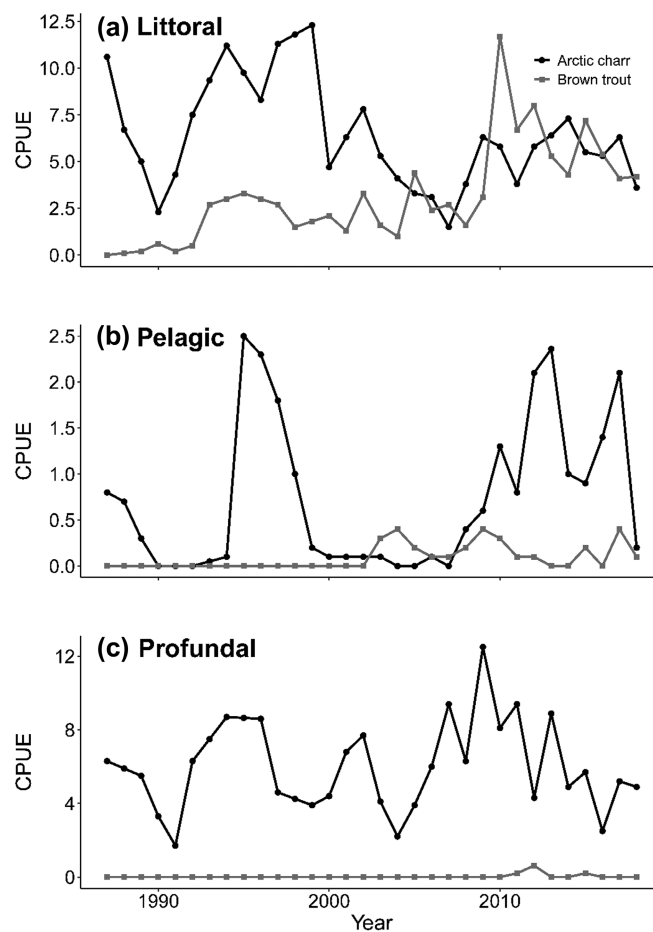


Figure 1. Density developments (CPUE, fish caught per 100 m<sup>2</sup> gillnet per night) of Arctic charr (black circles) and brown trout (grey squares) in the (a) littoral, (b) pelagic and (c) profundal habitats in Lake Takvatn from 1987 until 2018. Note the difference in scale on the y-axis.

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. 1990a). After successful attachment to the host the parasite goes through four larval stages (chalmus 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). *Salmincola edwardsii* is the only ectoparasite found on Arctic charr in Takvatn.

For each year of data, we estimated values of mean intensity (average number of female parasites per infected host), 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:

$$m_c = m + \frac{v}{m}$$

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 h. Each fish was wet-weighted ( $\pm 0.1$  g), had its fork length measured ( $\pm 0.1$  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 100 m<sup>2</sup> 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). Larger fish surface areas should provide bigger targets for copepodids to detect and hit, and additionally surface area is a better proxy for total gill area than length (Palzenberger and Pohla 1992). Fish length corresponds to the fork length (cm) and surface area (cm<sup>2</sup>) was estimated following the biomass-to-area conversion of 13.9 M<sup>0.61</sup> 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  $r=0.97$ ,  $p < 0.001$ ,  $df=6891$ ), but differed somewhat in their ability to predict *Salmincola* infections and therefore both measurements are included in separate models. Year-to-year changes in fish surface area are provided in the Supporting information.

### Water temperature

Historical climatological data was assessed following a one-dimensional air-to-water-temperature model (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 m 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 m of the water column over the months June, July, August and September as the predictor in our models. 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. The response variable parasite counts in individual fish was modelled with a negative binomial distribution with a log-link function to account for overdispersion using the *glmer.nb* function from the lme4 package in R (Bates et al.

2015). 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. 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. Marginal and conditional  $R^2$  values (Nakagawa et al. 2017) were calculated using the *tab\_model* function from the sjPlot package in R (Lüdtke 2020).

We further tested how the association between *S. edwardsii* abundance and fish size was related to 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. However, for contact-transmitted parasites, size rather than age at infection might be a more suitable metric for infection pressure (Dogiel 1961). Arctic charr age and length were highly correlated in our data ( $r=0.85$ ,  $p < 0.01$ ). 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. To calculate the force of infection, we first computed logistic regressions between Arctic charr length and parasite presence (infected versus uninfected) for each year individually (Supporting information). 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*. This measure can 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 pseudo-replicated 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 ( $\Delta$ ) 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  $\times$  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  $t$ ,  $t - 1$  and  $t - 2$  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

### Temporal trends in gill lice numbers, fish densities, body size and temperature

The overall prevalence of *Salmincola 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) (Fig. 2). Mean parasite intensity also varied across years, ranging between 1.1 (2003) and 8.1 (2018). The maximum number of gill lice recorded on a single fish was 69 in 1991 (see the Supporting information for parasite frequency distributions). 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). We observed the lowest density of Arctic charr across all habitats at the end of the culling period in 1990 and 1991, with another dip the mid-2000s. The highest density of charr in the littoral zone occurred between 1994 and 1999, and in the profundal habitat the density peaked in 2009. Brown trout density increased steadily throughout the study period

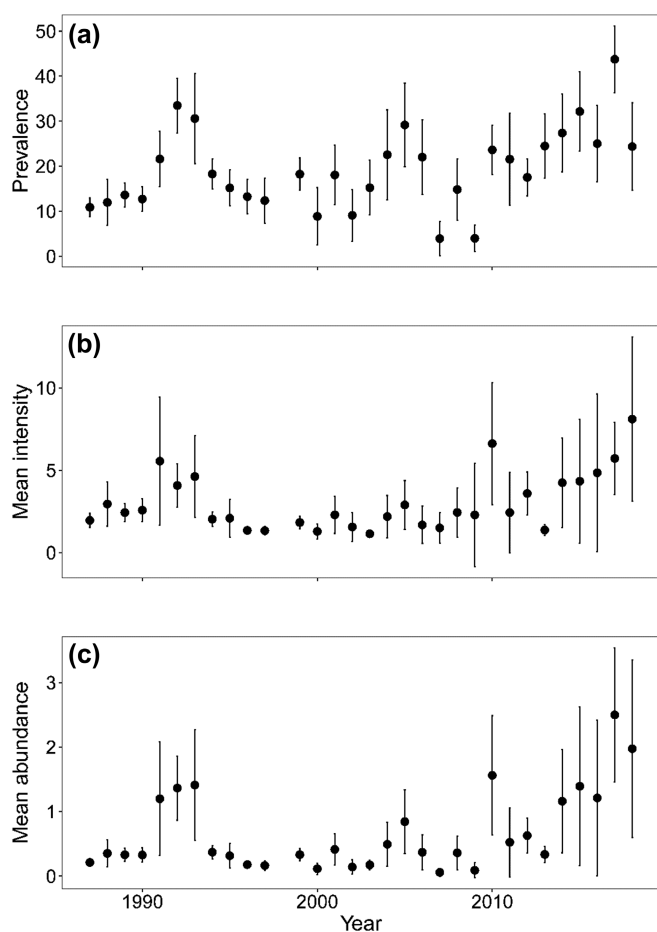


Figure 2. (a) Prevalence, (b) mean intensity and (c) mean abundance of *Salmincola edwardsii* infecting Arctic charr in Lake Takvatn from 1987 to 2018. Error bars indicate 95% confidence intervals.

(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 ( $r=0.07$ ,  $p=0.70$ ). The average body size of Arctic charr increased from 1987 to 1993, before declining until 2010, thereafter increasing during the last 10 years of the study period (Supporting information). There was no temporal trend in summer water temperature (linear regression, slope = 0.018,  $p=0.24$ ), with an average of 8.6°C across all years. The lowest average summer water temperature was 6.8°C in 1987, with the highest values being 10.0 and 9.9°C in 2002 and 2014, respectively (Supporting information).

### *Salmincola edwardsii* abundance increases with fish length

We found a clear positive relationship between Arctic charr body size (length) and *S. 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 ( $\Delta R^2=5.6$ , Supporting information). 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 force of infection – the fish length at which there was a 50% probability of parasite infection – varied from 254 mm (2016) to 391 mm (2003) (Fig. 3). The logistic regressions describing this relationship were significant for

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.

Predictors	<i>S. edwardsii</i> abundance		
	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			
$\sigma^2$		1.74	
$\tau_{00\_YEAR}$		0.22	
ICC		0.11	
$N_{YEAR}$		31	
Observations		6893	
Marginal R <sup>2</sup> / conditional R <sup>2</sup>		0.427/0.493	

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. 3). There was no effect of Arctic charr density or temperature in the current or previous year on the force of infection (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. 4, Table 2). Surface area was a better predictor of mean parasite abundance than mean fish length (lower AIC, Supporting information). An increase of 10  $\text{cm}^2$  in surface area (range 124–347  $\text{cm}^2$ ) 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. There was a similar effect of Arctic charr density in year  $t - 1$ , but the confidence interval included zero (Table 3). 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:

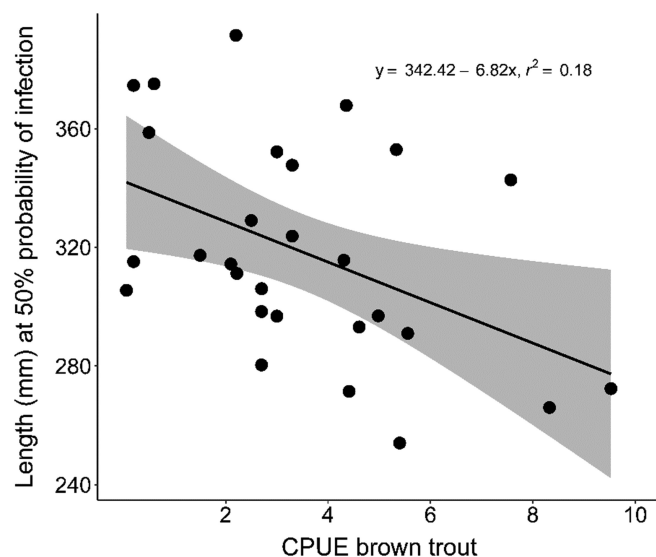


Figure 3. Length at which Arctic charr has a 50% probability of infection with *S. edwardsii* (retrieved from logistic regressions) as a function of brown trout density in Lake Takvatn for all years where the infection probability  $\sim$  length slope was statistically significant ( $p < 0.05$ , Supporting information). The shaded area represents the 95% confidence interval.

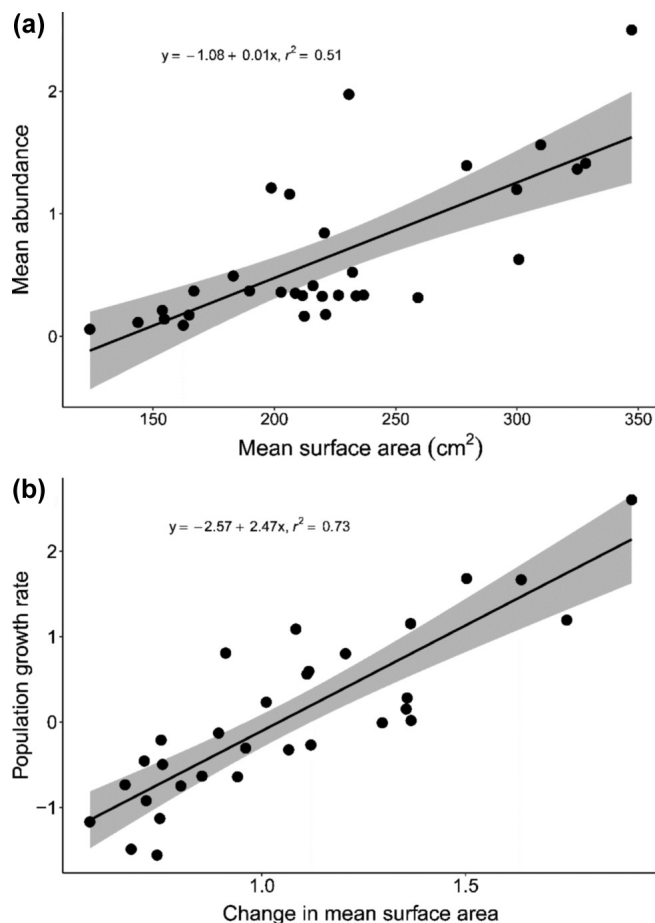


Figure 4. (a) Mean abundance of *S. edwardsii* as a function of mean body surface area of Arctic charr in every year sampled from 1987 to 2018 in Lake Takvatn. (b) *Salmincola edwardsii* population growth rate from year  $t - 1$  to  $t$  as a function of the relative change in mean body surface area from year  $t - 1$  to  $t$ . The shaded area represents the 95% confidence interval.

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  $t - 1$  (Supporting information).

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

Predictors	<i>S. edwardsii</i> mean abundance		
	Estimates	CI	p
(Intercept)	0.46	-0.21 to 1.12	0.190
Mean surface area <sub>year t</sub>	0.01	0.00–0.01	< <b>0.001</b>
Arctic charr density <sub>year t</sub>	-0.02	-0.04 to -0.01	<b>0.012</b>
Brown trout density <sub>year t</sub>	0.04	-0.01 to 0.08	0.114
Water temperature <sub>year t</sub>	-0.09	-0.19 to 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.

Predictors	<i>S. edwardsii</i> mean abundance		
	Estimates	CI	p
(Intercept)	-0.07	-2.23 to 2.08	0.946
Mean surface area <sub>year <math>t-1</math></sub>	-0.00	-0.00 to 0.00	0.116
Arctic charr density <sub>year <math>t-1</math></sub>	-0.02	-0.05 to 0.01	0.169
Brown trout density <sub>year <math>t-1</math></sub>	0.10	0.03–0.17	<b>0.010</b>
Water temperature <sub>year <math>t-1</math></sub>	0.19	-0.01 to 0.39	0.074
Observations	31		

### 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. 5). Brown trout density was autocorrelated with its own densities during the three preceding years (Fig. 5). *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. 5), 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 ( $p < 0.001$  Supporting information, Fig. 4). There were additional positive effects of brown trout density and mean crowding, which explained an additional 9% of the variation in parasite population growth (Supporting information). 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 population dynamics of the copepod parasite, and the host and parasite populations fluctuated independently of one another. Instead, the presence of the non-host intraguild

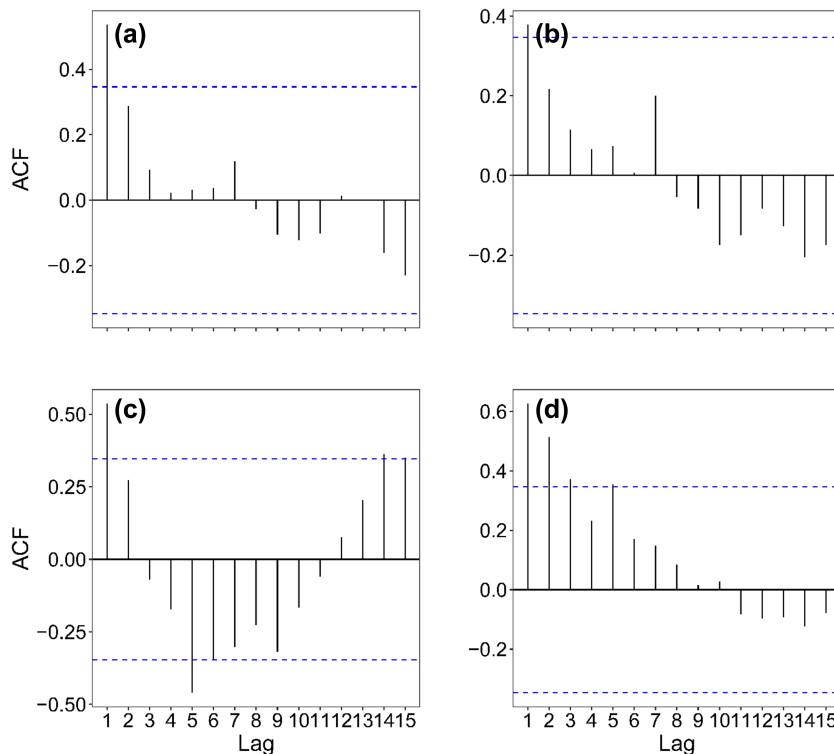


Figure 5. Autocorrelation functions (ACF) for the time series of *S. edwardsii* (a) mean abundance and (b) component population size, (c) Arctic charr density and (d) brown trout density. Dotted lines indicate where the autocorrelation is statistically significant ( $p < 0.05$ ).



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. The model for infection pressure had low predictive power compared to our other results. 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. 1990a, 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 could 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 (Lagrange 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 (Lagrange and Poulin 2015). There are few empirical long-term studies on host and parasite population dynamics from natural systems. Long-term studies of helminths in voles (Haukisalmi and Henttonen 1990) and acanthocephalans 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. 1990b, 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. Moreover, our results

could suggest that transmission mainly occurs in the profundal habitat, i.e. below the thermocline. If this is the case, fluctuating temperatures in the upper water layers will not affect parasite transmission. 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). In Takvatn, infections increased during the study period and are higher compared to other lake-dwelling Arctic charr populations in Norway (Kennedy 1978, Paterson et al. 2019). However, the potential for rapid parasite population growth in deep lakes is probably limited compared to stream-dwelling populations (Mitro 2016), or areas with aquaculture (Thorstad et al. 2015, Bøhn 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 some wild host populations fluctuating above this threshold, density may not be the main driver of parasite transmission.

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### Author contributions

**Eirik H. Henriksen:** Conceptualization (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Andre Fraimer:** Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Robert Poulin:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Rune Knudsen:** Conceptualization (supporting);

Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Per-Arne Amundsen:** Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9w0vt4bk7> (Henriksen et al. 2022).

### Supporting information

The Supporting information associated with this article is available with the online version.

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