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RESEARCH ARTICLE

Positive feedback between parasite infection and poor host body condition reduces host survival in the wild

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Abstract

1. Host–parasite relationships are ubiquitous on Earth. Although parasites reduce host health, parasite infections also occur due to compromised host health. Both causalities could induce positive feedback, in which infected hosts with poor body conditions may suffer further infection. Such positive feedback could increase host mortality and may finally affect host population dynamics. However, both causalities and how positive feedback affect host population dynamics has rarely been demonstrated in the wild, mainly due to methodological difficulties.
2. Here, we used a mark-recapture survey combined with structural equation modelling (SEM) to examine whether both causalities and positive feedback occurred in a host stream salmonid and parasitic copepod system. We also examined the factors affecting the apparent survival of hosts during the mark-recapture period using a Cormack–Jolly–Seber (CJS) model. Our target parasitic copepod *Salmincola markewitschi* is relatively large, attaching to the mouth cavity of host white-spotted charr *Salvelinus leucomaenis*, which enabled long-term tracking in natural conditions without sacrificing either host or parasite.
3. SEM using time-series snapshot data detected simultaneous occurrence of both causalities, that is the parasitic copepods reduced host body condition and host with poorer body condition were more likely infected by parasites, suggesting the positive feedback. Furthermore, the negative effects of parasites on host body condition were more frequently detected compared to the opposite causal link (high susceptibility to infections in hosts with poor body condition), and the strengths of both causal links fluctuated across seasons and initial infection statuses. The CJS model revealed that both parasite infection and poor host condition reduced apparent survival.
4. The mouth-attaching copepods might have reduced host body conditions by altering host foraging behaviour and/or inducing physiological costs such as immunity. High susceptibility in fish with poorer body condition was probably caused by low resource allocations to immunity and behavioural defences against

parasites. These direct and indirect processes should incur strong stresses to host fish, finally leading to higher mortality.

5. Our findings provided the first empirical evidence on how positive feedback between parasite infection and reduced host condition could influence the wild host population via reduction of host survival. Heavily infected hosts created by positive feedback may also play important roles in parasite spreading, for example, as a super spreader. Together, positive feedback would thus be important ecological processes to better understand host and parasite dynamics in the wild populations.

KEYWORDS
body condition, host–parasite relationship, infection dynamics, mark-recapture, path analysis, *Salmincola*, salmonid

1 | INTRODUCTION

Parasites account for more than one-third of species on Earth and a great amount of biomass in ecosystems (Dobson et al., 2008; Kuris et al., 2008; Lafferty et al., 2006); hence, host–parasite relationships are one of the most common biotic associations in nature (Carlson et al., 2020; Dobson et al., 2008; Hudson et al., 2006; Kuris et al., 2008). Parasites damage host health via directly exploiting resources from hosts or indirectly causing physiological burdens (Poulin, 2011; Sheldon & Verhulst, 1996) and can be major drivers of host evolutionary changes (Paterson et al., 2010) and host population dynamics (Hudson et al., 1998; Poulin, 2011). Parasite infections also occur due to poor host health (Beldomenico et al., 2008; Lochmiller, 1996; Pedersen & Greives, 2008). Given that gaining or maintaining immunity is nutritionally costly for hosts (Lochmiller, 1996; Sheldon & Verhulst, 1996), host individuals without enough food resources can be predisposed to higher parasite loads (Forbes et al., 2016). These opportunistic infections in epidemiology may cause parasite outbreaks and finally crush wild populations (Lochmiller, 1996). Therefore, parasite infections and host health synergistically affect wild host and parasite dynamics.

Elucidating the synergy of parasite infections and host body conditions in the wild can advance our understanding of wild host population dynamics. However, most field studies have only examined cross-sectional correlations and have discussed a one-sided causality (Beldomenico et al., 2008). Field studies finding a negative correlation between host body condition and infection parameters have generally interpreted that parasites are causes of poor host condition (Harper, 1999; Hasegawa, Ayer, et al., 2022; Sala-Bozano et al., 2012; Vicente et al., 2004): only a few studies suggested that poor condition such as food limitations may increase parasite prevalence and intensity because hosts compromise their immune functions under such situations (Forbes et al., 2016).

Most importantly, when parasite infections become both the cause and consequence of a poor host condition, a positive feedback occurs: an infected host with a poor body condition due to the parasite infection will be more susceptible to further infection (Beldomenico et al., 2008; Beldomenico & Begon, 2010; Beldomenico, Telfer, Gebert, et al., 2009; Beldomenico, Telfer, Lukomski, et al., 2009). This positive feedback is particularly important for understanding wild host population dynamics because this may increase prevalence of heavily infected hosts, which have low survival rate and eventually decrease the host population size (Beldomenico & Begon, 2010). Heavily infected hosts could be 'super spreaders' in the populations (Beldomenico & Begon, 2010), and thus this concept can also be important for parasites including disease dynamics (Beldomenico & Begon, 2010).

Both causalities and positive feedback are likely to occur in many natural host–parasite systems but these infection patterns and the consequences on host survival have rarely been demonstrated. This is probably because tracking small and cryptic parasite infections is usually difficult without sacrificing host individuals, although longitudinal studies are one of the best ways to infer the causalities in natural systems (Beldomenico et al., 2008; Godfrey et al., 2010; Telfer et al., 2010). Only few studies have overcome these problems and specifically tested causalities in wild conditions (Beldomenico et al., 2008; Blanchet et al., 2009; Dawson & Bortolotti, 2001; Godfrey et al., 2010). A series of studies by Beldomenico et al. (2008), Beldomenico, Telfer, Gebert, et al. (2009) and Beldomenico, Telfer, Lukomski, et al. (2009) successfully detected parasite infections on field voles *Microtus agrestis* in the field using a haematological method, and they monitored the infection status and host body condition combined with mark-recapture analysis of the host, clearly demonstrating positive feedback. A haemogram can be a useful indicator of infection; however, the authors did not observe parasites directly in the blood, and specific changes in infection intensity were not quantified. Blanchet et al. (2009) also demonstrated the causal relationships between parasite infections and host growth rates by estimating the growth of two host fishes from scales and otoliths, although these methods have potential estimation errors (e.g. Neilson, 1992), and the duration, frequency and intensity of parasites before sampling were not known. Moreover, Godfrey et al. (2010)

tested both causal links using tuatara *Sphenodon punctatus* and ectoparasite systems (ticks and mites). However, infections of these ectoparasites, which temporally attach to hosts, can change within a short period (Oliver, 1989), and this study consequently detected one-sided causality (i.e. negative effects of parasites on host body condition). Thus, previous findings have not sufficiently demonstrated the existence of condition–infection causality and positive feedback, necessitating more rigorous empirical evidence. Moreover, these previous studies did not evaluate host survival rate, even though positive feedback could likely cause host mortality in natural populations and, hence, affect wild host population dynamics (Beldomenico & Begon, 2010). Consequently, evidence for how positive feedback drives host population dynamics in the wild has rarely been available.

Here, we provide the first empirical evidence of both causalities, positive feedback and the consequences on host survival in wild populations by using a mark-recapture survey combined with structural equation modelling (SEM) in a wild stream fish–parasitic copepod system. SEM analysis is a powerful method for estimating the causalities in longitudinal datasets (Fan et al., 2016). In fact, several studies have applied this approach to longitudinal studies and have revealed complex natural interactions (Blanchet et al., 2009; Byrnes et al., 2011). Moreover, our focused ectoparasitic copepod, *Salmincola markewitschi*, is ideal for examining the causality between host body condition and parasite abundance because of their relatively large body size (2–7 mm; Hasegawa, Katahira, et al., 2022; Shedko & Shedko, 2002) and characteristic of attaching to the mouth cavities of host salmonid, white-spotted charr *Salvelinus leucomaenis* (Hasegawa, Katahira, et al., 2022; Shedko & Shedko, 2002), enabling us to visually track the change in infection intensity and host body condition over time without sacrificing host fish. Further, previous studies have suggested that *Salmincola* spp. have negative impacts on host fitness components, especially under rearing conditions, such as decline of fecundity (Gall et al., 1972), appetite (Hasegawa & Koizumi, 2023, 2024b; Hiramatsu et al., 2001; Nagasawa et al., 1994) and body condition (Hasegawa, Ayer, et al., 2022; Nagasawa et al., 1998). In a previous study by Hasegawa and Koizumi (2024a) also showed clear negative correlations between *S. markewitschi* loads and fish conditions in natural streams (Figure 1). Another parasite removal experiments showed that infections of *S. markewitschi* strongly reduced host body condition and growth rate through reduced feeding activities (Murakami et al., 2024). However, we still do not know whether poor host body condition affects parasite infections, and positive feedback occurs in the wild populations. Thus, we individually monitored the changes in inflection status, host body conditions and host survival in the Shiodomari River in southern Hokkaido, Japan.

2 | METHODS

2.1 | Study area

Mark-recapture surveys were conducted at the headwater tributary of the Ito River, Shiodomari River system, southern Hokkaido, Japan (41°83′ N, 140°98′ E). The study reach was 536 m, and it was divided into 22 sections (i.e. 25 m section × 21 + 11 m section × 1). The study reach was located between two waterfalls (both are about 2 m high under base flow condition). Since the waterfall prevents the upstream migration of most fish individuals (Hasegawa unpublished data), the population was considered as a closed system for the mark-recapture study. In addition, habitat above the upper waterfall was so marginal with few fish (Hasegawa personal observations) that immigration from upstream was negligible. The water temperature was recorded hourly with a HOBO data logger (Onset Computer Corporation, Bourne, MA, USA) from 2 June 2020 to 7 July 2021, and the average water temperature in the study reach was 8.4°C (min 0.0°C–max 18.9°C). All field surveys were conducted with the permission of the governor of Hokkaido, Japan (No. 2020–33, 2021–53). Our work did not require special permissions on animal welfare; however, all procedures were conducted according to Hokkaido University's animal experiments regulations.

2.2 | Study species

White-spotted charr (Figure 1) is a common salmonid fish inhabiting mountain streams in the Japanese archipelago (Hosoya, 2013). They live up to 10 years in the wild condition (Gudkov, 1992; Savvaitova et al., 2007). Like many other salmonids, they have two life history types in Hokkaido Island: some individuals remain and reproduce in their natal river throughout their lives (i.e. stream residents), whereas others migrate to the sea or lakes and later come back to the natal rivers for reproduction (i.e. migrants)

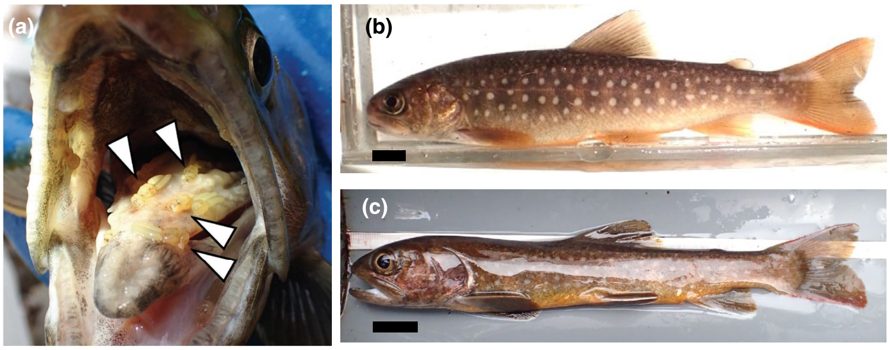

FIGURE 1 (a) *Salmincola markewitschi* (arrowhead) infecting the mouth cavity of white-spotted charr *Salvelinus leucomaenis*. (b) White-spotted charr not infected by copepods. (c) White-spotted charr infected by several copepods. Scale bars: 10 mm for (b) and 20 mm for (c).

(Morita, 2001; Morita et al., 2009). Above natural waterfalls or man-made dams, most individuals mature as residents (Morita et al., 2009). At our study site, some large sea-run migrants (less than twenty) passed the waterfall during the breeding season (Hasegawa unpublished data), but they were easily distinguished from stream residents due to their silvery colour, large body size and large white spots on the body surface (Ishigaki, 1984; Morita et al., 2009). Thus, we omitted the temporary, sporadic migrants from the data. No other fish species were observed in the study reach (Hasegawa unpublished data). Stream resident white-spotted charr showed high growth rates and body condition during early spring to summer (June–August) because of high food availability (Ishigaki, 1984; Morita et al., 2011).

In our study system, white-spotted charr have frequent infections by parasitic copepods in their mouth cavities (Hasegawa & Koizumi, 2021, 2023, 2024a). These copepods were identified as *Salmincola markewitschi* based on morphological observations and molecular analysis (Figure 1; Hasegawa, Katahira, et al., 2022; Shedko et al., 2023). Infections of *S. markewitschi* were observed year-around in this river system (Hasegawa & Koizumi, 2021, 2024a), with infection levels increasing from winter to spring and decreasing from summer to autumn (Hasegawa & Koizumi, 2024a). Although no detailed information about the life history of the target species is available, their relative species such as *S. californiensis* and *S. edwardsii* have direct life cycles with seven stages; nauplius, free-living copepodid (less than 1 mm; Kabata, 1969), chalimus 1–4 and mature adults (Conley & Curtis, 1993; Kabata & Cousens, 1973; Murphy et al., 2020; Stankowska-Radziun & Radziun, 1993). Infectious free-living copepodids live up to a few weeks (Conley & Curtis, 1993; Kabata & Cousens, 1973). During this short period, they find and attach to suitable hosts using shock waves and shadows produced by hosts as cues (Poulin et al., 1990). After the attachments, adult females infect hosts for at least 2 months, although their longevity was unknown (Kabata & Cousens, 1973; Murphy et al., 2020). Because all male copepods are a dwarf form attaching to female's body (Kabata & Cousens, 1973), we only counted females.

2.3 | Mark-recapture survey

Between 2 and 6 June 2020 (hereafter called 'June 2020'), we captured white-spotted charr by two-pass electrofishing using a backpack electrofisher unit (300 V DC, Model 12-B, Smith-Root Inc., Vancouver, WA, USA) and a dip net (2-mm mesh) at each section to estimate the charr abundance by the removal method (e.g. Riley & Fausch, 1992). Block nets (3-mm mesh) were set at the start and end points of each section to prevent fish from entering or leaving during electrofishing. Captured fish were anesthetised using FA100 (Bussan Animal Health Co., Ltd., Osaka, Japan), and body length (fork length; FL) and body weight (BW) were measured to the nearest 1 mm and 0.1 g, respectively. We checked for the presence and number of copepods by observing the fins, body surface and mouth cavity of each fish. Fluorescent elastomer tags (Northwest Marine Technology Inc., Shaw Island, WA, USA) were injected with a unique combination of six colours at four landmarks in each fish (two landmarks at the head and one point posterior to each eye). Photographs of all individuals were taken on the left side with a digital camera (TG4, Olympus, Tokyo, Japan) to ascertain the individual identification based on the variation of the white-spot pattern (Watz et al., 2019; Yagyu et al., 2007). After fish had recovered, we gently released the fish into the middle of each section from which they were captured. As age-0 fish were rarely infected by the copepod in a previous study (Hasegawa & Koizumi, 2021), we only captured and marked age-1 and older individuals.

Recapture occasions were conducted three times, given the parasite's life history described above (see 2.2) and due to some logistical reasons: July 2020 (4–9 July 2020), October 2020 (31 September–3 October 2020) and July 2021 (5–9 July). Fish were recaptured and treated in the same manner as the marking occasion (i.e. June 2020), except for the July 2021 survey, in which we captured fish by angling and two-pass electrofishing (Hasegawa & Koizumi, 2023). For individuals with fading elastomer colours or exhibiting body length shrinkage, we confirmed and identified them by checking the photographs (Watz et al., 2019; Yagyu et al., 2007). On these recapture occasions, we did not mark any new fish. Given the relatively long interval between October 2020 and July 2021 (i.e. 9 months), we did not use the data of July 2021 in the estimation of causality by SEM; however, they were used for the survival rate estimation (see Section 2.5.3; Figure 2). Data available from the figshare repository (https://doi.org/10.6084/m9.figshare.21868203.v1: Hasegawa et al., 2023).

2.4 | Replication statement

Our replication statement is outlined below.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Fish individuals ($N = 499$)	Fish individuals ($N = 499$)	Three time periods

2.5 | Statistical analyses

2.5.1 | Calculating variables

Following Bush et al.'s (1997) method, several infection parameters were calculated; prevalence (proportion of fish infected), abundance (the number of copepod individuals per examined fish), intensity (the number of copepod individuals per infected fish) and mean intensity (the average number of copepod individuals per infected fish). Charr abundance was estimated in each section using the removal method implemented in Program CAPTURE (White et al., 1978; available at https://www.mbr-pwrc.usgs.gov/software/capture.shtml). The host density in each section was

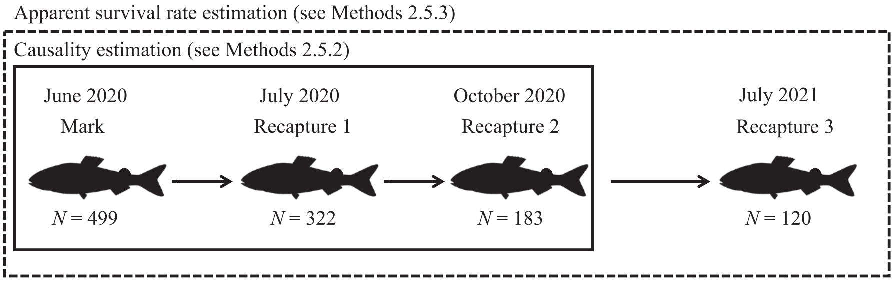

FIGURE 2 Summary of mark-recapture survey conducted from June 2020 until July 2021. *N* indicates the number of collected white-spotted charr. Refer to Table 1 for more information.

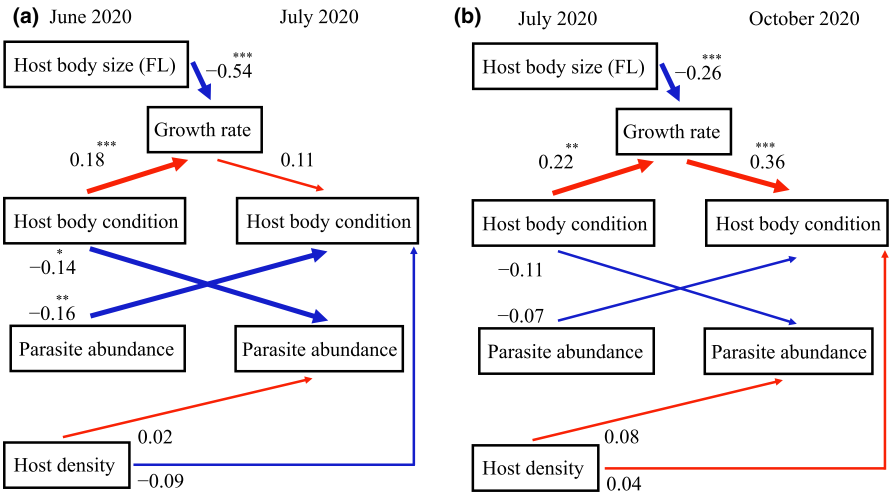

FIGURE 3 Causal relationships among factors of hosts and parasites inferred by piecewise SEM analysis. Standardized estimates were shown for each variable. (a) Results from June 2020 to July 2020. (b) Results from July 2020 to October 2020. Bold arrows indicate statistical significant effects (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$).

based on estimated charr abundance, and each section area (m^2) calculated from mean stream width and section length (i.e. 25 m or 11 m). For the host body condition, we used the residual index (Jakob et al., 1996): we calculated residual distances of individual points from the regression of ln (BW) against ln (FL). This body condition index is widely used in fish-parasite systems (Bagamian et al., 2004; Lagrue & Poulin, 2015; Perrot-Minnot et al., 2020). As fish body condition is assumed to be different among seasons in salmonids (e.g. Morita et al., 2011), we calculated residuals on each capture occasion (i.e. June 2020, July 2020, October 2020 and July 2021). We also calculated the growth rate (mm/day) for each host individual for each capture–recapture interval.

2.5.2 | Structural equation modelling

Structural equation modelling was performed using R 4.3.1 (R Core Team, 2023). To estimate the causalities among host body conditions, parasite infections and other possible factors, we used piecewise structural equation modelling using the package '*piecewise SEM*' version 2.3.0 (Lefcheck, 2016) based on the hypothetical scheme shown in Figure 3. Piecewise SEM allowed us to test the effects of parasite abundance and host body conditions on several parameters in subsequent months simultaneously. The whole model was composed of several generalized linear mixed-effects models (Lefcheck, 2016; Shipley, 2009). The goodness of fit of the whole model was evaluated by Shipley's test of direct separation using Fisher's *C* value (Lefcheck, 2016; Shipley, 2009). If that value did not fall below a significant level ($p < 0.05$), we considered that the model explained our datasets adequately. Since correlations, such as temporal correlations between parasite abundance and body conditions among occasions (Figure 3), severely reduced model fit, we treated these correlations as correlated errors (Lefcheck, 2016; Shipley, 2009). All linear mixed models in piecewise SEM were constructed using the package '*glmmTMB*' version 1.1.8 (Brooks et al., 2017), and all responses and explanatory variables were centred and scaled (mean = 0, SD = 1) before the analysis to allow us to directly compare the effects of each variable. We analysed data for each of two separate study periods (i.e. from June 2020 to July 2020 and from July 2020 to October 2020).

Based on the hypothetical schema, we constructed three linear mixed models. We expected that parasite abundance on the previous occasion would decrease host body condition on the next occasion (i.e. parasites are a cause of poor host condition; Figure 3). In addition, fish with higher growth rates would show higher body conditions, and high host density would decrease host body condition on the next occasion (Figure 3). Therefore, in the first model, the response variable was host body condition on the subsequent occasion, and explanatory variables were parasite abundance, host density and host growth rate on the current occasion. Parasite infections are likely to occur due to poor body condition (i.e. parasites are a consequence of poor condition; Figure 3). Parasite abundance could also be affected by host density on the previous occasion since higher host density contributes to parasite transmissions (Anderson & May, 1978). Thus, in the second model, the response variable was parasite abundance on the subsequent occasion, and

TABLE 1 Summary of host abundance, infection parameters and infection history at each capture–recapture event. Note that prevalence, mean intensity and mean fish fork length were calculated from marked fish.

	June 2020 (mark)	July 2020 (recapture 1)	October 2020 (recapture 2)	July 2021 (recapture 3)
Total host numbers (recapture rate)	499	322 (64.5%)	183 (36.7%)	120 (24.1%)
Prevalence (%)	36.5%	38.2%	31.1%	35.8%
Intensity range (mean)	1–9 (1.59)	1–11 (1.67)	1–6 (1.47)	1–6 (1.49)
Fork length range (mean)	69–226 (119.7)	82–219 (128.4)	83–220 (130.0)	103–220 (144.0)
Fish gained new parasite infections (%)[a]	*NA*	41 (12.7%)	31 (16.9%)	22 (18.3%)
Fish experienced parasite detachments (%)[b]	*NA*	59 (18.3%)	45 (24.6%)	15 (12.5%)

Note: Both calculations were conducted only using fish recaptured on consecutive occasions. For instance, % calculations in October 2020 were based on fish recaptured in both July 2020 and October 2020.

[a] Number of fish which gained new parasite infections (fish showing increments of parasite abundance) from the previous occasion to the current occasion/total number of fish recaptured.

[b] Number of fish which experienced parasite detachments (fish showing decline in parasite abundance) from the previous occasion to the current occasion/total number of fish recaptured.

the explanatory variables were body condition and host density on the current occasion (Figure 3). Finally, because host body size (FL) and body condition on the previous occasion affect host growth rate (Gabelhouse Jr, 1991; Morita, 2001; Figure 3), we constructed another model that included growth rate as the response variable, with its explanatory variables being body condition and body size on the previous occasion. The study sections and fish individual ID were included as random effects in all models.

To further confirm whether the predicted causal links were detected under different situations, we conducted additional analyses using subsets of the datasets using SEM and generalized linear mixed models (GLMMs) (Appendices S1 and S2). We considered the relationship was significant if the *p*-value was ≤0.05 and marginally significant if the *p*-value was 0.05–0.10.

2.5.3 | Cormack–Jolly–Seber model

Survival probability of white-spotted charr between sampling occasions was estimated by Cormack–Jolly–Seber (CJS) models (Lebreton et al., 1992) using the Bayesian state-space approach (Kéry & Schaub, 2012). We assumed that individual *i* survived from occasion *t* to occasion *t*+1 with a survival probability that differed by occasion and individual:

$$z_{i,t+1} \mid z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}\,\phi_{i,t}\right)$$

$$\text{logit}\left(\phi_{i,t}\right) = \alpha 0_t + \alpha 1_t * \text{ForkLength}_{i,t} + \alpha 2 * \text{BodyCondition}_{i,t} + \alpha 3 * \text{ParasiteAbundance}_{i,t},$$

The latent state variable was binary, where $z_{i,t} = 1$ if individual *i* was alive on occasion *t*, and 0 if dead. We modelled individual- and interval-specific survival probability, $\phi_{i,t}$, as a function of fork length, body condition and parasite abundance of individual *i* on occasion *t*. The covariates were standardized by mean divided by standard deviation on each occasion, so that the intercept, $\alpha 0_t$, was the predicted survival probability of an individual with average values of these covariates on occasion *t* on the logit scale. Missing values of the covariates were not allowed in this model, although data could not be collected on sampling occasions when individuals could not be captured. Therefore, missing fork length values were imputed by developing a simple linear regression model using fork length values of the individuals captured between two consecutive sampling occasions (Appendix S3). Missing values of body condition and parasite abundance were imputed with their mean values on each occasion (i.e. 0) because strong predictive relationships between the two consecutive occasions did not exist for the two covariates. We let the fork length effect on survival to vary by occasion ($\alpha 1_t$) but the effects of body condition and parasite abundance to be time constant ($\alpha 2$ and $\alpha 3$) because their posterior distributions overlapped greatly among sampling occasions (Appendix S4). Three individuals suffered handling mortality on the second occasion (July 2020) and two additional individuals on the third occasion (October 2020), and these individuals were excluded from survival estimation after their known mortality events.

Because electrofishing and angling cannot capture all individuals present in the study reach, we modelled capture probability ($p_{i,t}$) of individual *i* on occasion *t* using fork length as a covariate:

$$y_{i,t} \mid z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}\,p_{i,t}\right)$$

$$\text{logit}\left(p_{i,t}\right) = \beta 0_t + \beta 1 * \text{ForkLength}_{i,t}$$

where $y_{i,t}$ is the capture-history data (1 if captured, 0 if not) of individual *i* on occasion *t*, $\beta 0_t$ is an occasion-specific intercept, and $\beta 1$ is a time-constant effect of fork length on capture probability because their posterior distributions overlapped greatly among sampling occasions in a different model with time-varying effects of fork length (Appendix S4). Fork length was standardized by mean, so that $\beta 0_t$ is the capture probability of average-sized individuals on occasion *t* on the logit scale.

Parameters of survival and recapture probabilities were modelled as fixed effects, and survival and capture probabilities cannot be independently estimated in the last sampling interval in the CJS model (Kéry & Schaub, 2012). Because additional information on capture probabilities was available from two-pass removal electrofishing on each sampling occasion, we used them to constrain the capture probability of white-spotted charr on the last sampling occasion (July 2021). Specifically, we assumed that the capture probability was similar between the two preceding occasions (July and October 2020; $\beta 0_1 = \beta 0_2$), when only electrofishing was conducted. We estimated capture probabilities of white-spotted charr using a removal method (Zippin, 1958) and found that the capture probability was approximately 7% higher in July 2021, when angling occurred prior to electrofishing ($\beta 0_3 > \beta 0_1 = \beta 0_2$), relative to July and October 2020 (Appendix S5: $\mathrm{logit}^{-1}(\beta 0_3) = \mathrm{logit}^{-1}(\beta 0_1) \times 1.07$). We incorporated this information in the CJS model to estimate the survival and capture probabilities individually in the last sampling interval.

Survival probability depends on sampling interval lengths. For the direct comparison of these probabilities among capture–recapture intervals, we standardized survival at the monthly scale to align with the shortest capture–recapture period (i.e. from June 2020 to July 2020). We calculated monthly mean survival and 95% credible intervals as (CJS-based survival probability)$^{1/3}$ from July 2020 to October 2020 (i.e. 3 months) and (CJS-based survival probability)$^{1/9}$ from October 2020 to July 2021 (i.e. 9 months). In this analysis, we assumed that survival probabilities were constant throughout each interval.

We fit CJS models using a Markov chain Monte Carlo (MCMC) method in Program JAGS (Plummer, 2017) called from R 4.3.0 (R Core Team, 2023) with the jagsUI package. Diffuse priors were used throughout in the Bayesian approach. Posterior distributions of model parameters were characterized by taking every 10th sample from 20,000 iterations of four chains after a burn-in period of 10,000 iterations. Models were assumed to have converged when the R-hat statistic was <1.1 for all model parameters (Gelman & Hill, 2007). We report 95% credible intervals (CRI) and the proportion of posterior samples with the same sign as the posterior mean (i.e. *f* value in JAGS output) and use both metrics to evaluate covariate effects on survival and capture probabilities.

3 | RESULTS

In total, we marked 499 fish in June 2020, of which 322 (recapture rate 64.5%), 183 (36.7%) and 120 fish (24.1%) were recaptured in July 2020, October 2020 and July 2021, respectively. Infection parameters, infection patterns and fish body size during the mark-recapture occasion are summarized in Figure 2 and Table 1.

From June 2020 to July 2020, the hypothesised model constructed by piecewise SEM fit our data adequately (Fisher's $C = 5.52$, $p = 0.06$; Figure 3a). Consistent with our initial predictions, parasite abundance on the previous occasion negatively affected body condition on the current occasion, suggesting that parasite infections reduced host body condition (i.e. parasites are a cause of poor host condition; Figure 3a). Body condition on the previous occasion also negatively affected parasite abundance on the current occasion, suggesting that host with poor body condition were likely to gain further infections, as predicted (i.e. parasites are a consequence of poor host condition; Figure 3a). Fish with higher body conditions exhibited higher growth rates (Figure 3a), and smaller fish showed higher growth rate, as indicated by negative correlation between growth rates and body size (Figure 3a). Contrary to our initial predictions, host density did not affect either body condition and parasite abundance (Figure 3a).

From July 2020 to October 2020, the model also fit the data reasonably (Fisher's $C = 7.63$, $p = 0.11$; Figure 3b). Contrary to our initial predictions, neither parasite abundance nor host body condition on the previous occasion negatively affected host body condition and parasite abundance on the current occasion (i.e. parasites are neither a cause nor consequence of poor host condition Figure 3b). Fish with higher body condition showed higher growth rate, and fish that showed higher growth rates had higher body conditions on the subsequent occasion (Figure 3b). Similar to the previous sampling interval (i.e. June 2020 to July 2020), smaller fish showed higher growth rate (Figure 3b). Host density did not have significant effects on other variables (Figure 3b).

These predicted causal links between host body condition and parasite infections were generally supported by additional analyses using subsets of the data, although the model performance was better in the original models (Appendices S1 and S2). Several GLMMs showed that copepod infections reduced host body condition and growth rate, even after accounting for several factors such as previous body condition (Appendix S1). Additionally, we found that poor body condition increased susceptibility to infections, although this relationship was supported by only one model, suggesting that this causal link was comparatively weaker than the opposite link (i.e. the negative effects of copepods). Furthermore, the additional SEMs using subsets of the data also detected several predicted causal links (Appendix S2), with these trends being particularly evident among hosts that were initially infected (Appendix S2). SEMs that did not support the predicted causal links generally showed lower model fit values (Appendix S2).

CJS models revealed that survival probability of white-spotted charr changed over time to align with sampling interval lengths. Posterior mean probability of survival was 0.91 (95% CRI: 0.85, 0.97) from June to July 2020, 0.81 (0.74, 0.88) from July to October 2020, and 0.46 (0.39, 0.53) from October 2020 to July 2021. Standardized survival probabilities for 1 month did not differ among sampling intervals: 0.93 (0.90, 0.96) from July to October 2020 and 0.92 (0.90, 0.93) from October 2020 to July 2021. Mean capture probability was estimated to be 0.73 (0.69, 0.78) in July and October 2020 when only electrofishing was conducted, and 0.79 (0.74, 0.83) when both angling and electrofishing were used.

Survival differed based on individual covariates (Figure 4). As predicted, individuals with better body condition were more likely to survive (Figure 4; $\alpha 2 = 0.21$; $f = 97\%$), although their 95% CRI just overlapped with 0 (0, 0.44). Survival decreased with higher

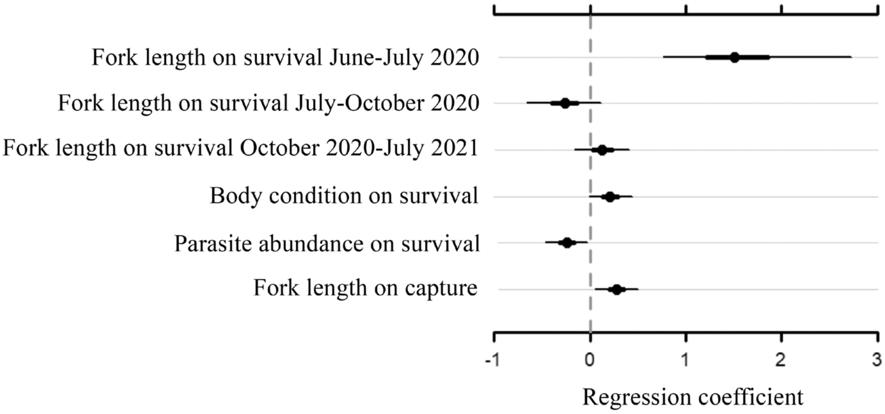

FIGURE 4 Covariate effects on survival and capture probability of white-spotted charr in the Cormack–Jolly–Seber model. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals. A vertical dotted line is drawn at 0 (i.e. no effect).

parasite abundance (Figure 4; $\alpha3 = -0.24$ [95% CRI: −0.46, −0.02 and $f = 98\%$]). Larger charr were more likely to survive than smaller charr from June to July 2020 (Figure 4; $\alpha1_1 = 1.55$ [95% CRI: 0.75, 2.63 and $f = 100\%$]), but body size effect was much weaker from July to October 2020 (Figure 4; $\alpha1_2 = -0.27$ [95% CRI: −0.68, 0.11 and $f = 91\%$]) and from October 2020 to July 2021 (Figure 4; $\alpha1_3 = 0.13$ [95% CRI: −0.15, 0.42 and $f = 83\%$]). Larger charr were more catchable than smaller charr (Figure 4; $\beta1 = 0.28$ [95% CRI: 0.05, 0.51 and $f = 99\%$]).

4 | DISCUSSION

Many studies have suggested the negative impacts of parasites on wild host populations, but most reported simple correlations and hence overlooked causal relationships (Harper, 1999; Hasegawa, Ayer, et al., 2022; Sala-Bozano et al., 2012; Vicente et al., 2004). This is probably due to methodological difficulties in the long-term tracking of host individuals and parasite infections. Only a few studies have explicitly tested the causality, but these studies indirectly estimated infections and host fitness (Beldomenico et al., 2008; Beldomenico, Telfer, Gebert, et al., 2009; Beldomenico, Telfer, Lukomski, et al., 2009; Blanchet et al., 2009; Dawson & Bortolotti, 2001), and often failed to detect both causal links (Godfrey et al., 2010). Our study, by contrast, directly monitored the changes in infection intensity, host body condition and growth rate by the mark-recapture method, and therefore, provides more rigorous evidence on the plausible causal relationships and positive feedback in wild populations. Further, our study found both poor body condition and infection reduced host survival, suggesting that positive feedback could affect host population dynamics via increased mortality.

As predicted, we found that fish with poor body condition were likely to suffer parasite infections. One possible mechanism of this high susceptibility is low resource allocations to immunity. The body condition index, including our index based on body weight-length relationships, generally represents the host's overall health status, energy budget and immune functions (Sanchez et al., 2018; Wilder et al., 2016). Although hosts commonly cope with parasite infections using innate and adaptive immune systems (Fast, 2014; Graham et al., 2011), developing and maintaining these systems are very costly (Lochmiller, 1996; Sheldon & Verhulst, 1996), and therefore hosts with poor conditions, attributable to parasite infections, cannot allocate their resources to immunity, resulting in higher parasite intensity. Our study suggests this mechanism.

Behavioural differences depending on host body condition also explain high susceptibility to parasites in fish with poor body condition. Animals often show anti-parasite tactics such as dispersal from infection sources (Brown et al., 2016; Terui et al., 2017) and 'parasite-removing behaviours' such as substrate rubbing (Atkinson et al., 2018; Kabata & Cousens, 1977). However, these behaviours are commonly considered energy dependent (Bonte et al., 2012; Krohn & Boisclair, 1994; Terui et al., 2017); thus, hosts with poor conditions cannot employ these tactics. Hosts with poorer body condition might also show poor activity and movement (Kanno et al., 2023), and therefore, these fish are easily infected by parasites with low-swimming ability (but see discussions below).

We found that parasite infections reduced host body condition in our study system, though this pattern was observed only from June 2020 to July 2020. Several additional analyses also supported this pattern (Appendix S2). This effect was particularly pronounced in fish infected by two or more copepods, suggesting that the negative impact of parasites was intensity-dependent (Appendix S1). Because our study copepods generally attach to the host's mouth cavity, their infections can physically impair host foraging and subsequently reduce body condition and growth (Hasegawa & Koizumi, 2023, 2024a, 2024b; Murakami et al., 2024; Nagasawa et al., 1994). Indeed, our parasite removal experiments demonstrated significant reductions in feeding, leading to a marked decline in body condition and growth in white-spotted charr infected with the same copepod species (Murakami et al., 2024). A series of studies by Hasegawa and Koizumi (2023, 2024b) further highlighted profound effects of these copepods on host foraging and competitive abilities. Therefore, loss of body condition and growth in our study system is likely attribute to feeding impediments by copepod infections, and this pattern becomes clearer in heavily infected fish, as physical inhibition and behavioural modifications by parasites are generally intensity-dependent (Sala-Bozano et al., 2012; Shirakashi & Goater, 2002). Another possible mechanism contributing to the observed reduction in body condition is the energetic cost associated with immune response and tissue repair following infections. *Salmincola* spp. cause tissue damage, such as gill destructions and mouth cavity swellings (Hasegawa, Ayer, et al., 2022; Kabata & Cousens, 1977; Nagasawa et al., 1998). Both the activation of immune defences and the repair of damaged tissues require significant energy expenditure (White et al., 2020), which can ultimately compromise host body condition (Hasegawa, Ayer, et al., 2022). These costs are typically greater in fish showing higher infection intensities (Bleay et al., 2007; Costello, 2006).

Taken together, our results demonstrate that positive feedback occurs in the wild population: an infected host with a poor body condition due to the parasite infection will be more susceptible to further infection. Based on our discussions above, we could infer how positive feedback works in our study system. When fish with poor body condition are infected with parasites, these fish could not remove parasites due to lower resource allocations to immunity and behavioural defences (Bonte et al., 2012; Krohn & Boisclair, 1994; Lochmiller, 1996; Sheldon & Verhulst, 1996). Infected parasites continuously reduce host body condition via feeding impediments (Hasegawa & Koizumi, 2023, 2024b; Murakami et al., 2024), causing physical damages and activating costly immunity, thereby increasing susceptibility to further parasites, and so on. Additionally, intraspecific competition and subsequent habitat shifts in fish with poor body conditions might also explain positive feedback in our study system. Salmonids exhibit a strong dominance hierarchy (Fausch et al., 2021; Nakano, 1995), and poor conditioned (and/or parasitized) fish could be outcompeted by other conspecifics in these intraspecific competitions (Hasegawa & Koizumi, 2024b; Nakano, 1995). Alternatively, some fish consequently experience poorer body condition by being outcompeted. In either way, outcompeted fish may be forced to move outside of the most profitable habitat at the centre of the stream flow, where dominant fish occupy and defend (Nakano, 1995). In low-velocity environments occupied by outcompeted individuals, free-swimming copepodids may easily attach to the hosts (Monzyk et al., 2015). Under these circumstances, positive feedback can readily occur.

Most importantly, we found that both body condition and parasite abundance significantly predicted host apparent survival rates, suggesting that positive feedback could ultimately undermine the host population through the reduced host survival (Beldomenico & Begon, 2010). Therefore, our results supported, for the first time, the Beldomenico and Begon's (2010) hypothesis that positive feedback drives wild host populations. Given that body condition is continuously reduced as positive feedback occurs, host body condition eventually fails to meet the threshold for maintaining critical physiological and physical functions such as metabolism. In particular, this positive feedback may significantly reduce host survival during the winter period since overwintering often requires considerable energy to survive (Hurst, 2007; Huusko et al., 2007). However, we found that standardized survival probabilities did not differ among periods, indicating that host survival is seasonally consistent. Thus, harsh conditions in winter do not appear the main reason for the poor survival of infected hosts in our study case.

Several biological interactions indirectly reduce the host survival rate. For instance, heavily infected hosts, generally in poor condition, are likely to be preyed upon predators (Møller & Erritzøe, 2000; Temple, 1987). These heavily infected hosts are also prone to being outcompeted by conspecifics (Barber et al., 2000; Filipsson et al., 2018), which reduces their access to food resources and available shelters. Further, these fish may be vulnerable to flooding events, which often result in salmonid fish mortality (Seegrist & Gard, 1972; Weese et al., 2011). Recapturing at shorter intervals would provide more information on factors affecting host survival through positive feedback.

We acknowledge that several cautions be required when interpreting our results, as these were not always consistent among analyses. First, we found different outcomes between study periods; both causalities were detected during the first capture–recapture period (i.e. from June 2020 to July 2020) but not during the subsequent period (i.e. from July 2020 to October 2020). This discrepancy may partly stem from fish maturation, which could obscure the condition–infection relationship. The breeding season of white-spotted charr is September and October in the study area (Morita, 2001) and fish allocate more resources to gonadal development during the second period rather than anti-parasite efforts, such as increasing immunity. Another possible explanation is a temporal mismatch between the biological processes and the study interval. The second period was relatively long (i.e. 3 months) and some fish might have ameliorated their body condition or experienced the detachments of copepods. A 3-month period may also allow a seasonal change in infection dynamics. In fact, infection levels decreased from July to October (approximately 7%, Table 1), as reported in a previous study conducted in the same river system (Hasegawa & Koizumi, 2024a). These temporal changes in fish and parasite dynamics could obscure the negative effects of parasites on hosts. Furthermore, fluctuations in resource availability may have contributed to these results, although the specific mechanisms remain unclear. The abundance of aquatic invertebrates is generally high in spring and early summer, whereas the flux of terrestrial invertebrates from forests increases later in the season (e.g. Nakano & Murakami, 2001). Seasonal differences in food resource quantity and quality can differentially affect host body condition and immune function (McNew et al., 2019; Wilcoxen et al., 2015), potentially influencing the dynamics of host health and parasite infection.

Second, one causal link—poor body condition increasing susceptibility to infections—was generally weak and, in some cases, absent (Appendices S1 and S2). This suggests that susceptibility to parasite infections may be influenced not only by host body condition but also by other factors. For instance, in some host–parasite systems, mobile hosts are more susceptible to infections than less mobile ones (Fuxjager et al., 2011; Poulin et al., 1991), as mobile hosts encounter the infective stages of parasites more frequently (Fuxjager et al., 2011). Infective stages can also locate mobile hosts more easily because they generally find hosts using environmental cues, such as shock waves (Lawrence, 1981; Poulin et al., 1990). Given that host body condition is often correlated with host activity levels (Kanno et al., 2023; Sih et al., 2015), fish with better body condition may paradoxically be more susceptible to infections. Moreover, susceptibility to parasite infections can also be influenced by genetic factors and/or random processes (Lysne & Skorping, 2002; Morrill & Forbes, 2012). These unmeasured factors could have affected our results, masking the predicted causal links.

However, these inconsistencies rather provide valuable insights into the dynamics of positive feedback. For example, we can hypothesise that positive feedback is likely to start from poor body condition resulting from parasite infections, rather than from the high susceptibility to infections due to poor body condition. As discussed, although poor body condition is an important determinant of susceptibility (Beldomenico et al., 2008), other factors or random processes may also play significant roles. Regardless of the causes, once hosts are infected, body condition deteriorates rapidly because the negative effects of the copepods are strong (Murakami et al., 2024). This reduced body condition facilitates further infections, initiating a feedback loop. Our additional SEMs supported this hypothesis; both causal links were significant when focusing on fish that were already infected at the initial capture, whereas these links were not significant for fish without infections at the marking occasion (Appendix S2). It remains unclear whether similar patterns would be observed in positive feedback processes in other host–parasite systems, because the factors affecting susceptibility and virulence can vary across systems (Poulin, 2011). Thus, further case studies in different host–parasite systems are required to deepen our understanding of how positive feedback operates in wild populations.

Positive feedback should be taken into account when considering host–parasite dynamics because this concept may also work at the (meta-)population level (Beldomenico & Begon, 2010). Beldomenico and Begon (2010) predicted that the populations with a large proportion of individuals in poor conditions are likely to have a higher prevalence and infection intensity, and this also increases the risk of further infections to other local populations via dispersal. Because average body condition and immune ability vary among populations (Becker et al., 2020; Cornet et al., 2009), such predictions are likely to occur in natural systems. Further, positive feedback may eventually cause host death, as discussed above, so this may affect host population dynamics. In this context, high infection levels observed during winter in our study system (Hasegawa & Koizumi, 2024a) could be explained by this population-level positive feedback. Poorer host body condition in winter (Hasegawa & Koizumi, 2024a; Morita et al., 2011) likely increases susceptibility to infections, leading to high infection prevalence within populations. Moreover, environmental changes, such as climate change or urbanization, often reduce host body condition and/or increase parasite infection (Becker et al., 2020; Beldomenico & Begon, 2015), likely triggering feedback at population levels (Beldomenico & Begon, 2015). Testing the patterns and processes of positive feedback is essential for understanding host and parasite dynamics, which also provide significant implications for population and disease management.

AUTHOR CONTRIBUTIONS

All authors conceived the idea and study design. Field works were conducted by Ryota Hasegawa, Yasuhiko Otsuki, Yohsuke Uemura, Chiharu Furusawa, Masahiro Naka. Ryota Hasegawa and Yoichiro Kanno conducted data analyses. Ryota Hasegawa wrote the first draft of the manuscript, and all authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

We declare no competing interests.

DATA AVAILABILITY STATEMENT

The data are available from Figshare: https://doi.org/10.6084/m9.figshare.21868203.v1 (Hasegawa et al., 2023).

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REFERENCES

Anderson, R. M., & May, R. M. (1978). Regulation and stability of host-parasite population interactions: I. Regulatory processes. *The Journal of Animal Ecology*, *47*, 219–247. https://doi.org/10.7208/chicago/9780226125534-034

Atkinson, E. M., Bateman, A. W., Dill, L. M., Krkošek, M., Reynolds, J. D., & Godwin, S. C. (2018). Oust the louse: Leaping behaviour removes sea lice from wild juvenile sockeye salmon *Oncorhynchus nerka*. *Journal of Fish Biology*, *93*, 263–271. https://doi.org/10.1111/jfb.13684

Bagamian, K. H., Heins, D. C., & Baker, J. A. (2004). Body condition and reproductive capacity of three-spined stickleback infected with the cestode *Schistocephalus solidus*. *Journal of Fish Biology*, *64*, 1568–1576. https://doi.org/10.1111/j.0022-1112.2004.00411.x

Barber, I., Hoare, D., & Krause, J. (2000). Effects of parasites on fish behaviour: A review and evolutionary perspective. *Review of Fish Biology and Fisheries*, *10*, 131–165. https://doi.org/10.1023/A:1016658224470

Becker, D. J., Albery, G. F., Kessler, M. K., Lunn, T. J., Falvo, C. A., Czirják, G. Á., Martin, L. B., & Plowright, R. K. (2020). Macroimmunology: The drivers and consequences of spatial patterns in wildlife immune defence. *Journal of Animal Ecology*, *89*, 972–995. https://doi.org/10.1111/1365-2656.13166

Beldomenico, P. M., & Begon, M. (2010). Disease spread, susceptibility and infection intensity: Vicious circles? *Trends in Ecology & Evolution*, *25*, 21–27. https://doi.org/10.1016/j.tree.2009.06.015

Beldomenico, P. M., & Begon, M. (2015). Stress-host-parasite interactions: A vicious triangle? *Revista FAVE. Sección Ciencias Veterinarias*, *14*, 6–19.

Beldomenico, P. M., Telfer, S., Gebert, S., Lukomski, L., Bennett, M., & Begon, M. (2008). Poor condition and infection: A vicious circle in natural populations. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1753–1759. https://doi.org/10.1098/rspb.2008.0147

Beldomenico, P. M., Telfer, S., Gebert, S., Lukomski, L., Bennett, M., & Begon, M. (2009). The vicious circle and infection intensity: The case of *Trypanosoma microti* in field vole populations. *Epidemics*, *1*, 162–167. https://doi.org/10.1016/j.epidem.2009.05.002

Beldomenico, P. M., Telfer, S., Lukomski, L., Gebert, S., Bennett, M., & Begon, M. (2009). Host condition and individual risk of cowpox virus infection in natural animal populations: Cause or effect? *Epidemiology and Infection*, *137*, 1295–1301. https://doi.org/10.1017/S0950268808001866

Blanchet, S., Méjean, L., Bourque, J. F., Lek, S., Thomas, F., Marcogliese, D. J., Dodson, J. J., & Loot, G. (2009). Why do parasitized hosts look different? Resolving the "chicken-egg" dilemma. *Oecologia*, *160*, 37–47. https://doi.org/10.1007/s00442-008-1272-y

Bleay, C., Wilkes, C. P., Paterson, S., & Viney, M. E. (2007). Density-dependent immune responses against the gastrointestinal nematode *Strongyloides ratti*. *International Journal for Parasitology*, *37*, 1501–1509. https://doi.org/10.1016/j.ijpara.2007.04.023

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, M. J. (2012). Costs of dispersal. *Biological Review*, *87*, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zeroinflated generalized linear mixed modeling. *The R Journal*, *9*, 378400.

Brown, G. P., Kelehear, C., Pizzatto, L., & Shine, R. (2016). The impact of lungworm parasites on rates of dispersal of their anuran host, the invasive cane toad. *Biological Invasions*, *18*, 103–114. https://doi.org/10.1007/s10530-015-0993-1

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, *83*, 575–583. https://doi.org/10.2307/3284227

Byrnes, J. E., Reed, D. C., Cardinale, B. J., Cavanaugh, K. C., Holbrook, S. J., & Schmitt, R. J. (2011). Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biology*, *17*, 2513–2524. https://doi.org/10.1111/j.1365-2486.2011.02409.x

Carlson, C. J., Dallas, T. A., Alexander, L. W., Phelan, A. L., & Phillips, A. J. (2020). What would it take to describe the global diversity of parasites? *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20201841.

Conley, D. C., & Curtis, M. A. (1993). Effects of temperature and photoperiod on the duration of hatching, swimming, and copepodid survival of the parasitic copepod *Salmincola edwardsii*. *Canadian Journal of Zoology*, *71*, 972–976.

Cornet, S., Biard, C., & Moret, Y. (2009). Variation in immune defence among populations of *Gammarus pulex* (Crustacea: Amphipoda). *Oecologia*, *159*, 257–269. https://doi.org/10.1007/s00442-008-1211-y

Costello, M. J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, *22*, 475–483. https://doi.org/10.1016/j.pt.2006.08.006

Dawson, R. D., & Bortolotti, G. R. (2001). Sex-specific associations between reproductive output and hematozoan parasites of American kestrels. *Oecologia*, *126*, 193–200. https://doi.org/10.1007/s004420000506

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F., & Jetz, W. (2008). Homage to Linnaeus: How many parasites? How many hosts? *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 11482–11489. https://doi.org/10.1073/pnas.0803232105

Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S. R., Park, H., & Shao, C. (2016). Applications of structural equation modeling (SEM) in ecological studies: An updated review. *Ecological Processes*, *5*, 1–12. https://doi.org/10.1186/s13717-016-0063-3

Fast, M. D. (2014). Fish immune responses to parasitic copepod (namely sea lice) infection. *Developmental and Comparative Immunology*, *43*, 300–312. https://doi.org/10.1016/j.dci.2013.08.019

Fausch, K. D., Nakano, S., Kitano, S., Kanno, Y., & Kim, S. (2021). Interspecific social dominance networks reveal mechanisms promoting coexistence in sympatric charr in Hokkaido, Japan. *Journal of Animal Ecology*, *90*, 515–527. https://doi.org/10.1111/1365-2656.13384

Filipsson, K., Petersson, T., Höjesjö, J., Piccolo, J. J., Näslund, J., Wengström, N., & Österling, E. M. (2018). Heavy loads of parasitic freshwater pearl mussel (*Margaritifera margaritifera* L.) larvae impair foraging, activity and dominance performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, *27*, 70–77. https://doi.org/10.1111/eff.12324

Forbes, K. M., Mappes, T., Sironen, T., Strandin, T., Stuart, P., Meri, S., Vapalahti, O., Henttonen, H., & Huitu, O. (2016). Food limitation constrains host immune responses to nematode infections. *Biology Letters*, *12*, 20160471. https://doi.org/10.1098/rsbl.2016.0471

Fuxjager, M. J., Foufopoulos, J., Diaz-Uriarte, R., & Marler, C. A. (2011). Functionally opposing effects of testosterone on two different types of parasite: Implications for the immunocompetence handicap hypothesis. *Functional Ecology*, *25*, 132–138. https://doi.org/10.1111/j.1365-2435.2010.01784.x

Gabelhouse, D. W., Jr. (1991). Seasonal changes in body condition of white crappies and relations to length and growth in Melvern Reservoir, Kansas. *North American Journal of Fisheries Management*, *11*, 50–56. https://doi.org/10.1577/1548-8675(1991)011<0050:SCIBCO>2.3.CO;2

Gall, G. A. E., Mcclendon, E. L., & Schafer, W. E. (1972). Evidence on the influence of the copepod (*Salmincola californiensis*) on the reproductive performance of a domesticated strain of rainbow trout (*Salmo gairdneri*). *Transactions of the American Fisheries Society*, *101*, 345–346. https://doi.org/10.1577/1548-8659(1972)101<345:EOTIOT>2.0.CO;2

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press.

Godfrey, S. S., Moore, J. A., Nelson, N. J., & Bull, C. M. (2010). Unravelling causality from correlations: Revealing the impacts of endemic ectoparasites on a protected species (tuatara). *Parasitology*, *137*, 275–286. https://doi.org/10.1017/S0031182009991314

Graham, A. L., Shuker, D. M., Pollitt, L. C., Auld, S. K., Wilson, A. J., & Little, T. J. (2011). Fitness consequences of immune responses: Strengthening the empirical framework for ecoimmunology. *Functional Ecology*, *25*, 5–17. https://doi.org/10.1111/j.1365-2435.2010.01777.x

Gudkov, P. K. (1992). Data on the biology of the Far Eastern char, *Salvelinus leucomaenis*, in the Sea of Okhotsk basin. *Journal of Ichthyology*, *32*, 9–23.

Harper, D. G. (1999). Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Animal Behaviour*, *58*, 553–562. https://doi.org/10.1006/anbe.1999.1154

Hasegawa, R., Ayer, C. G., Umatani, Y., Miura, K., Ukumura, M., Katahira, H., & Koizumi, I. (2022). Potential negative effects and heterogeneous distribution of a parasitic copepod *Salmincola edwardsii* (Copepoda: Lernaeopodidae) on Southern Asian Dolly Varden *Salvelinus curilus* in Hokkaido, Japan. *Parasitology International*, *87*, 102529. https://doi.org/10.1016/j.parint.2021.102529

Hasegawa, R., Katahira, H., & Koizumi, I. (2022). *Salmincola markewitschi* (Copepoda: Lernaeopodidae) or *S. carpionis*? A requirement for taxonomic revision due to their high morphological variations. *Folia Parasitologica*, *69*, 025. https://doi.org/10.14411/fp.2022.025

Hasegawa, R., & Koizumi, I. (2021). Relative importance of host-dependent versus physical environmental characteristics affecting the distribution of an ectoparasitic copepod infecting the mouth cavity of stream salmonid. *Ecological Research*, *36*, 1015–1027. https://doi.org/10.1111/1440-1703.12262

Hasegawa, R., & Koizumi, I. (2023). Parasites either reduce or increase host vulnerability to fishing: A case study of a parasitic copepod and its salmonid host. *The Science of Nature*, *110*, 10. https://doi.org/10.1007/s00114-023-01836-x

Hasegawa, R., & Koizumi, I. (2024a). Consistent negative correlations between parasite infection and host body condition across seasons suggest potential harmful impacts of *Salmincola markewitschi* on wild white-spotted charr, *Salvelinus leucomaenis*. *Zoological Science*, *41*, 192–200. https://doi.org/10.2108/zs230028

Hasegawa, R., & Koizumi, I. (2024b). Do mouth-infecting parasites alter the foraging ecology of host fish? A test with the parasitic copepod *Salmincola markewitschi* and white-spotted charr *Salvelinus leucomaenis*. *Freshwater Biology*, *70*, e14362. https://doi.org/10.1111/fwb.14362

Hasegawa, R., Otsuki, Y., Uemura, Y., Furusawa, C., Naka, M., & Koizumi, I. (2023). Hasegawa_et_al_MarkRecapture of whitespotted charr. *Figshare*, Dataset. https://doi.org/10.6084/m9.figshare.21868203.v1

Hiramatsu, N., Fukada, H., Kitamura, M., Shimizu, M., Fuda, H., Kobayashi, K., & Hara, A. (2001). Serum immunoglobulin M (IgM) in Sakhalin Taimen (*Hucho perryi*). *Aquaculture Science*, *49*, 347–355. https://doi.org/10.11233/aquaculturesci1953.49.347

Hosoya, K. (2013). Salmonidae. In T. Nakabo (Ed.), *Fishes of Japan with pictorial keys to the species* (3rd ed., pp. 362–367). Tokai University Press. (In Japanese).

Hudson, P. J., Dobson, A. P., & Lafferty, K. D. (2006). Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology & Evolution*, *21*, 381–385. https://doi.org/10.1016/j.tree.2006.04.007

Hudson, P. J., Dobson, A. P., & Newborn, D. (1998). Prevention of population cycles by parasite removal. *Science*, *282*, 2256–2258. https://doi.org/10.1126/science.282.5397.2256

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, *71*, 315–345. https://doi.org/10.1111/j.1095-8649.2007.01596.x

Huusko, A. R. I., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Koljonen, S., Louhi, P., & Alfredsen, K. (2007). Life in the ice lane: The winter ecology of stream salmonids. *River Research and Applications*, *23*, 469–491. https://doi.org/10.1002/rra.999

Ishigaki, K. (1984). *Exploring the mystery of Charrs*. Iwanami-Shoten. (In Japanese).

Jakob, E. M., Marshall, S. D., & Uetz, G. W. (1996). Estimating fitness: A comparison of body condition indices. *Oikos*, *77*, 61–67. https://doi.org/10.2307/3545585

Kabata, Z. (1969). Revision of the genus *Salmincola* Wilson, 1915 (Copepoda: Lernaeopodidae). *Journal of Fisheries Board on Canada*, *26*, 2987–3041. https://doi.org/10.1139/f69-285

Kabata, Z., & Cousens, B. (1973). Life cycle of *Salmincola californiensis* (Dana 1852) (Copepoda: Lernaeopodidae). *Journal of Fisheries Board on Canada*, *30*, 881–903. https://doi.org/10.1139/f73-150

Kabata, Z., & Cousens, B. (1977). Host–parasite relationships between sockeye salmon, *Oncorhynchus nerka*, and *Salmincola californiensis* (Copepoda: Lernaeopodidae). *Journal of the Fisheries Board of Canada*, *34*, 191–202. https://doi.org/10.1139/f77-029

Kanno, Y., Locklear, M. L., Platis, N. M., & Lewis, S. T. (2023). Body condition metrics explain fish movement in experimental streams. *Journal of Zoology*, *320*, 18–28. https://doi.org/10.1111/jzo.13049

Kéry, M., & Schaub, M. (2012). *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Academic Press.

Krohn, M. M., & Boisclair, D. (1994). Use of stereo video system to stimate the energy expenditure of free-swimming fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 1119–1127. https://doi.org/10.1139/f94-111

Kuris, A. M., Hechinger, R. F., Shaw, J. C., Whitney, K. L., Aguirre-Macedo, L., Boch, C. A., Dobson, A. P., Dunham, E. J., Fredensborg, B. L., Huspeni, T. C., Lorda, J., Mababa, L., Mancini, F. T., Mora, A. B., Pickering, M., Talhouk, N. L., Torchin, M. E., & Lafferty, K. D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, *454*, 515–518. https://doi.org/10.1038/nature06970

Lafferty, K. D., Dobson, A. P., & Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 11211–11216. https://doi.org/10.1073/pnas.0604755103

Lagrue, C., & Poulin, R. (2015). Measuring fish body condition with or without parasites: Does it matter? *Journal of Fish Biology*, *87*, 836–847. https://doi.org/10.1111/jfb.12749

Lawrence, P. O. (1981). Host vibration—A cue to host location by the parasite, Biosteres longicaudatus. *Oecologia*, *48*, 249–251. https://doi.org/10.1007/BF00347971

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*, 67–118. https://doi.org/10.2307/2937171

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210X.12512

Lochmiller, R. L. (1996). Immunocompetence and animal population regulation. *Oikos*, *76*, 594–602. https://doi.org/10.2307/3546356

Lysne, D. A., & Skorping, A. (2002). The parasite *Lernaeocera branchialis* on caged cod: Infection pattern is caused by differences in host susceptibility. *Parasitology*, *124*, 69–76. https://doi.org/10.1017/S0031182001008848

McNew, S. M., Knutie, S. A., Goodman, G. B., Theodosopoulos, A., Saulsberry, A., Yépez, R. J., Bush, S. E., & Clayton, D. H. (2019). Annual environmental variation influences host tolerance to parasites. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20190049. https://doi.org/10.1098/rspb.2019.0049

Møller, A. P., & Erritzøe, J. (2000). Predation against birds with low immunocompetence. *Oecologia*, *122*, 500–504. https://doi.org/10.1007/s004420050972

Monzyk, F. R., Friesen, T. A., & Romer, J. D. (2015). Infection of juvenile salmonids by *Salmincola californiensis* (Copepoda: Lernaeopodidae) in reservoirs and streams of the Willamette River basin, Oregon. *Transactions of the American Fisheries Society*, *144*, 891–902. https://doi.org/10.1080/00028487.2015.1052558

Morita, K. (2001). The growth history of anadromous white-spotted charr in northern Japan: A comparison between river and sea life. *Journal of Fish Biology*, *59*, 1556–1565. https://doi.org/10.1111/j.1095-8649.2001.tb00220.x

Morita, K., Morita, S. H., & Nagasawa, T. (2011). Seasonal changes in stream salmonid population densities in two tributaries of a boreal river in northern Japan. *Ichthyological Research*, *58*, 134–142. https://doi.org/10.1007/s10228-010-0201-3

Morita, K., Morita, S. H., & Yamamoto, S. (2009). Effects of habitat fragmentation by damming on salmonid fishes: Lessons from white-spotted charr in Japan. *Ecological Research*, *24*, 711–722. https://doi.org/10.1007/s11284-008-0579-9

Morrill, A., & Forbes, M. R. (2012). Random parasite encounters coupled with condition-linked immunity of hosts generate parasite aggregation. *International Journal for Parasitology*, *42*, 701–706. https://doi.org/10.1016/j.ijpara.2012.05.002

Murakami, L., Hasegawa, R., Aruga, N., Sato, N., Nakamura, S., Kajihara, H., & Koizumi, I. (2024). Mouth-attaching copepod *Salmincola* *markewitschi* reduces the body condition and growth of juvenile salmonid *Salvelinus leucomaenis* by decreasing host feeding activity: Evidence from parasite removal experiment. *bioRxiv*. 2024.10.08.617322 https://doi.org/10.1101/2024.10.08.617322

Murphy, C. A., Gerth, W., & Arismendi, I. (2020). Hatching and survival of the salmon 'gill maggot' *Salmincola californiensis* (Copepoda: Lernaeopodidae) reveals thermal dependence and undocumented naupliar stage. *Parasitology*, *147*, 1338–1343. https://doi.org/10.1017/S0031182020001109

Nagasawa, K., Ikuta, K., Nakamura, H., Shikama, T., & Kitamura, S. (1998). Occurrence and effects of the parasitic copepod *Salmincola carpionis* on salmonids in the Nikko District, Central Japan. *Journal of Marine Systems*, *15*, 269–272. https://doi.org/10.1016/S0924-7963(97)00062-6

Nagasawa, K., Watanabe, J. R., Kimura, S., & Hara, A. (1994). Infection of *Salmincola stellatus* (Copepoda: Lernaeopodidae) on Sakhalin taimen *Hucho perryi* reared in Hokkaido. *Bulletin of Fisheries Sciences, Hokkaido University*, *45*, 109–112.

Nakano, S. (1995). Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Canadian Journal of Zoology*, *73*, 1845–1854. https://doi.org/10.1139/z95-217

Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 166–170. https://doi.org/10.1073/pnas.98.1.166

Neilson, J. D. (1992). Sources of error in otolith microstructure examination. Otolith microstructure examination and analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *117*, 115–125.

Oliver, J. H. (1989). Biology and systematics of ticks (Acari: Ixodida). *Annual Review of Ecology and Systematics*, *20*, 397–430. https://www.jstor.org/stable/2097098

Paterson, S., Vogwill, T., Buckling, A., Benmayor, R., Spiers, A. J., Thomson, N. R., Quail, M., Smith, F., Walker, D., Libberton, B., Fenton, A., Hall, N., & Brockhurst, M. A. (2010). Antagonistic coevolution accelerates molecular evolution. *Nature*, *464*, 275–278. https://doi.org/10.1038/nature08798

Pedersen, A. B., & Greives, T. J. (2008). The interaction of parasites and resources cause crashes in a wild mouse population. *Journal of Animal Ecology*, *77*, 370–377. https://doi.org/10.1111/j.1365-2656.2007.01321.x

Perrot-Minnot, M. J., Bollache, L., & Lagrue, C. (2020). Distribution of *Pomphorhynchus laevis* s.l. (Acanthocephala) among fish species at a local scale: Importance of fish biomass density. *Journal of Helminthology*, *94*, e99. https://doi.org/10.1017/S0022149X1900097X

Plummer, M. (2017). *JAGS version 4.3.0 user manual*.

Poulin, R. (2011). *Evolutionary ecology of parasites* (2nd ed.). Princeton University Press.

Poulin, R., Curtis, M. A., & Rau, M. E. (1990). Responses of the fish ectoparasite *Salmincola edwardsii* (Copepoda) to stimulation, and their implication for host-finding. *Parasitology*, *100*, 417–421. https://doi.org/10.1017/S0031182000078707

Poulin, R., Curtis, M. A., & Rau, M. E. (1991). Size, behaviour, and acquisition of ectoparasitic copepods by brook trout, *Salvelinus fontinalis*. *Oikos*, *61*, 169–174. https://doi.org/10.2307/3545334

R Core Team. (2023). *R: A language and environment for statistical computing*. R foundation for statistical computing.

Riley, S. C., & Fausch, K. D. (1992). Underestimation of trout population size by maximum-likelihood removal estimates in small streams. *North American Journal of Fisheries Management*, *12*, 768–776. https://doi.org/10.1577/1548-8675(1992)012<0768:UOTPSB>2.3.CO;2

Sala-Bozano, M., Van Oosterhout, C., & Mariani, S. (2012). Impact of a mouth parasite in a marine fish differs between geographical areas. *Biological Journal of the Linnean Society*, *105*, 842–852. https://doi.org/10.1111/j.1095-8312.2011.01838.x

Sanchez, C. A., Becker, D. J., Teitelbaum, C. S., Barriga, P., Brown, L. M., Majewska, A., Hall, R. J., & Altizer, S. (2018). On the relationship between body condition and parasite infection in wildlife: A review and meta-analysis. *Ecology Letters*, *21*, 1869–1884. https://doi.org/10.1111/ele.13160

Savvaitova, K. A., Kuzishchin, K. V., Pichugin, M. Y., Gruzdeva, M. A., & Pavlov, D. S. (2007). Systematics and biology of the East Siberian char *Salvelinus leucomaenis*. *Journal of Ichthyology*, *47*, 53–66. https://doi.org/10.1134/S0032945207010067

Seegrist, D. W., & Gard, R. (1972). Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society*, *101*, 478–482. https://doi.org/10.1577/1548-8659(1972)101<478:EOFOTI>2.0.CO;2

Shedko, M. B., & Shedko, S. V. (2002). Parasitic copepods of the genus *Salmincola* (Lernaeopodidae) from the far eastern chars *Salvelinus* (Salmonidae) with description of the new species *S. markewitschi*. *Zoologicheskiĭ Zhurnal*, *81*, 141–153. [In Russian, with English abstract].

Shedko, S. V., Shedko, M. B., Miroshnichenko, I. L., & Nemkova, G. A. (2023). DNA identification of parasitic copepods *Salmincola* (Copepoda, Siphonostomatoida, Lernaeopodidae): Variability and rate of evolution of the mitochondrial cytochrome c oxidase subunit I gene. *Russian Journal of Genetics*, *59*, 1022–1031. https://doi.org/10.1134/S1022795423100113

Sheldon, B. C., & Verhulst, S. (1996). Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, *11*, 317–321. https://doi.org/10.1016/0169-5347(96)10039-2

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*, 363–368. https://doi.org/10.1890/08-1034.1

Shirakashi, S., & Goater, C. P. (2002). Intensity-dependent alteration of minnow (*Pimephales promelas*) behavior by a brain-encysting trematode. *Journal of Parasitology*, *88*, 1071–1074. https://doi.org/10.1645/0022-3395(2002)088[1071:IDAOMP]2.0.CO;2

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state – behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, *30*(1), 50–60. https://doi.org/10.1016/j.tree.2014.11.004

Stankowska-Radziun, M., & Radziun, K. (1993). Observations on the development of *Salmincola edwardsii* (Olsson, 1869) (Copepoda: Lernaeopodidae) parasitizing the Arctic charr (*Salvelinus alpinus* (L.)) in the Hornsund region (Vest Spitsbergen). *Acta Ichthyologica et Piscatoria*, *23*, 107–114. (In Russian with English abstract).

Telfer, S., Lambin, X., Birtles, R., Beldomenico, P., Burthe, S., Paterson, S., & Begon, M. (2010). Species interactions in a parasite community drive infection risk in a wildlife population. *Science*, *330*, 243–246. https://doi.org/10.1126/science.1190333

Temple, S. A. (1987). Do predators always capture substandard individuals disproportionately from prey populations? *Ecology*, *68*, 669–674. https://doi.org/10.2307/1938472

Terui, A., Ooue, K., Urabe, H., & Nakamura, F. (2017). Parasite infection induces size-dependent host dispersal: consequences for parasite persistence. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171491. https://doi.org/10.1098/rspb.2017.1491

Vicente, J., Fierro, Y., Martinez, M., & Gortazar, C. (2004). Long-term epidemiology, effect on body condition and interspecific interactions of concomitant infection by nasopharyngeal bot fly larvae (*Cephenemyia auribarbis* and *Pharyngomyia picta*, Oestridae) in a population of Iberian red deer (*Cervus elaphus hispanicus*). *Parasitology*, *129*, 349–361. https://doi.org/10.1017/S0031182004005578

Watz, J., Otsuki, Y., Nagatsuka, K., Hasegawa, K., & Koizumi, I. (2019). Temperature-dependent competition between juvenile salmonids in small streams. *Freshwater Biology*, *64*, 1534–1541. https://doi.org/10.1111/fwb.13325

Weese, D. J., Schwartz, A. K., Bentzen, P., Hendry, A. P., & Kinnison, M. T. (2011). Eco-evolutionary effects on population recovery following catastrophic disturbance. *Evolutionary Applications*, *4*, 354–366. https://doi.org/10.1111/j.1752-4571.2010.00169.x

White, C. F., Gray, M. A., Kidd, K. A., Duffy, M. S., Lento, J., & Monk, W. A. (2020). Prevalence and intensity of *Salmincola edwardsii* in brook trout in northwest New Brunswick, Canada. *Journal of Aquatic Animal Health*, *32*, 11–20. https://doi.org/10.1002/aah.10091

White, G. C., Burnham, K. P., Otis, D. L., & Anderson, D. R. (1978). *User's manual for program CAPTURE*. Utah State University Press.

Wilcoxen, T. E., Horn, D. J., Hogan, B. M., Hubble, C. N., Huber, S. J., Flamm, J., Knott, M., Lundstrom, L., Salik, F., Wassenhove, S. J., & Wrobel, E. R. (2015). Effects of bird-feeding activities on the health of wild birds. *Conservation Physiology*, *3*, cov058. https://doi.org/10.1093/conphys/cov058

Wilder, S. M., Raubenheimer, D., & Simpson, S. J. (2016). Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Functional Ecology*, *30*, 108–115. https://doi.org/10.1111/1365-2435.12460

Yagyu, M., Nakamura, H., & Miyazaki, T. (2007). A method for identifying individual Japanese charr, *Salvelinus leucomaenis*, using parr marks. *Japanese Journal of Ichthyology*, *54*, 187–196. (In Japanese with English abstract).

Zippin, C. (1958). The removal method of population estimation. *The Journal of Wildlife Management*, *22*, 82–90. https://doi.org/10.2307/3797301

SUPPORTING INFORMATION

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

Appendix S1. Additional GLMM analyses for testing causal relationships among variables.

Appendix S2. Additional structural equation modeling (SEM) for testing causal relationships among variables.

Appendix S3. Estimation of missing fork length values for Cormack–Jolly–Seber model.

Appendix S4. An additional Cormack-Jolly-Seber model.

Appendix S5. Estimation of capture probabilities on each recapture occasion.

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