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Tapeworm Parasite Burden Is Linked to Diet, Body Size, Condition, Growth, Restocking and Habitat Use in Piscivorous Salmonids of a Subarctic Lake

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ABSTRACT

Parasites affect hosts in interaction with the entire ecological community. This is particularly evident for trophically transmitted parasites, such as *Dibothriocephalus* tapeworms, which infect multiple intermediate fish hosts, potentially reducing their fitness and suitability for human consumption. Here, we used a large, multi-year dataset to examine ecological underpinnings between *Dibothriocephalus* burden and host traits and diet. In particular, we assessed relationships between parasite burden and body size, body condition, growth, restocking origin and stomach contents in the key piscivorous salmonids, Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*), in a large subarctic lake, Lake Inari. We found that *Dibothriocephalus* prevalence was similarly high in both salmonids, with decreasing parasite burden over the years. In both species, larger individuals and those having three-spined (*Gasterosteus aculeatus*) and/or ninespine (*Pungitius pungitius*) stickleback remnants in their stomachs had a higher parasite burden, whereas better body condition, quicker growth, stomach contents other than sticklebacks, stocked origin (in Arctic charr) and river habitat (in brown trout) were associated with lower parasite counts. These findings suggest that *Dibothriocephalus* burden is likely to be costly, while successful foraging on non-stickleback food is associated with lower burden. Overall, the results highlight the intricacy of trophic accumulation of *Dibothriocephalus* parasites, with sticklebacks playing a special role in their transmission.

1 | Introduction

Parasites are ubiquitous in animal communities, including those of fishes, and play an important role in shaping the community structure (Marcogliese 2004; Lagrue et al. 2011; Tompkins et al. 2011; Timi and Poulin 2020). By altering host physiology, behaviour and survival, parasites influence not only specific host species but also their interactions with other species within the ecosystem (Marcogliese 2004; Lafferty 2008; Tompkins et al. 2011). From an economic perspective, high parasite burdens in fishes can reduce catches, lower their recreational or commercial value, and, in some cases, increase the risk of transmission to humans (Kuchta et al. 2013).

The congeneric tapeworms (Cestoda) *Dibothriocephalus ditremus* and *D. dendriticus* (previously known as *Diphyllobothrium dendriticum*: Waeschenbach et al. 2017) commonly infect salmonid fishes across their circumpolar distribution (Curtis and Bylund 1991; Kuchta et al. 2013). Their life cycle involves birds (especially *Larus* gulls) and mammals as final hosts, copepods as first hosts, small fishes as intermediate hosts and larger piscivorous fishes as secondary intermediate hosts (Knudsen et al. 2008; Henriksen et al. 2016; Kuhn et al. 2016; Prati et al. 2020). In northern Europe, the fish hosts include sticklebacks (Gasterosteidae), coregonids and piscivorous salmonids (Rahkonen and Koski 1997; Knudsen et al. 2008; Kuhn et al. 2016). In the salmonid hosts, *Dibothriocephalus* tapeworms

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may cause tissue inflammation, reduced growth and changes in muscles (Rahkonen and Koski 1997; Blanar et al. 2005). In regions where these tapeworms are common, they can also infect humans via the consumption of raw or undercooked fish (Curtis and Bylund 1991; Kuchta et al. 2013).

Because *Dibothriocephalus* species are transmitted trophically, their infection risk and intensity are likely to depend on the potential host's prey selection and other dietary factors (Rahkonen and Koski 1997; Kahilainen and Lehtonen 2003; Henriksen et al. 2016; Kuhn et al. 2016). Moreover, the parasite burden may increase over time with the cumulative transmission by consumption of infected prey. Consequently, spatial or temporal shifts in prey fish species composition may influence their numbers in piscivorous intermediate hosts. Environmental factors may further modulate these patterns. For example, predicted increase in temperatures in the high latitudes can alter parasite transmission and dynamics, partly by affecting the abundance and distribution of host species (Streppavara et al. 2018; Casas-Mulet et al. 2021; Lauringson et al. 2021).

Two culturally significant salmonid species, the Arctic charr (*Salvelinus alpinus*) and the brown trout (*Salmo trutta*) form an iconic species pair in many subarctic lakes (Kangosjärvi et al. 2024). When allopatric, they occupy relatively similar ecological niches, but when coexisting within the same lake, brown trout typically dominate, while Arctic charr become restricted to epiphentic or pelagic habitats, with both significant overlap and divergence in prey selection (Kahilainen and Lehtonen 2002; Gregersen et al. 2006; Knudsen et al. 2008). Both species commonly shift to piscivory as they grow, provided that suitable prey fish are sufficiently abundant (L'Abée-Lund et al. 2002; Amundsen 1994; Kahilainen and Lehtonen 2002; Jensen et al. 2015; Kangosjärvi et al. 2026). This dietary transition has the potential to facilitate the transmission of parasites, such as *Dibothriocephalus* tapeworms (Henriksen et al. 2016; Kuhn et al. 2016), which commonly parasitise both species (Knudsen et al. 2008; Henriksen et al. 2016).

Here, we used a large, multi-year dataset to examine the trophic dynamics underlying *Dibothriocephalus* burden in Arctic charr and brown trout in a large subarctic lake, Lake Inari, where salmonids have historically experienced high rates of *Dibothriocephalus* infection (Heinimaa and Salonen 2005). Specifically, we investigated how parasite burden relates to host stomach contents, body size and body condition. We also examined temporal trends across seasons and over the study period, differences between the two host species, effects on growth, associations with restocking, and, for brown trout, the influence of habitat type (lake versus river).

2 | Materials and Methods

2.1 | Study Site

The study was conducted using fish samples from a large ($> 1000\,\text{km}^2$) subarctic lake, Lake Inari, and from two rivers discharging into it (Figure 1). The lake's fish community comprises 10 native and three introduced species, of which seven are salmonids and the Arctic charr and the brown trout are the dominant piscivorous salmonids (Salonen 2004, 2021; Alioravainen et al. 2025). According to the present dataset, their most important prey species in the lake include small individuals of the European whitefish (*Coregonus lavaretus*), vendace (*Coregonus albula*), three-spined stickleback (*Gasterosteus aculeatus*), nine-spine stickleback (*Pungitius pungitius*), as well as invertebrates. Of these, the vendace is not native to Lake Inari; the species was

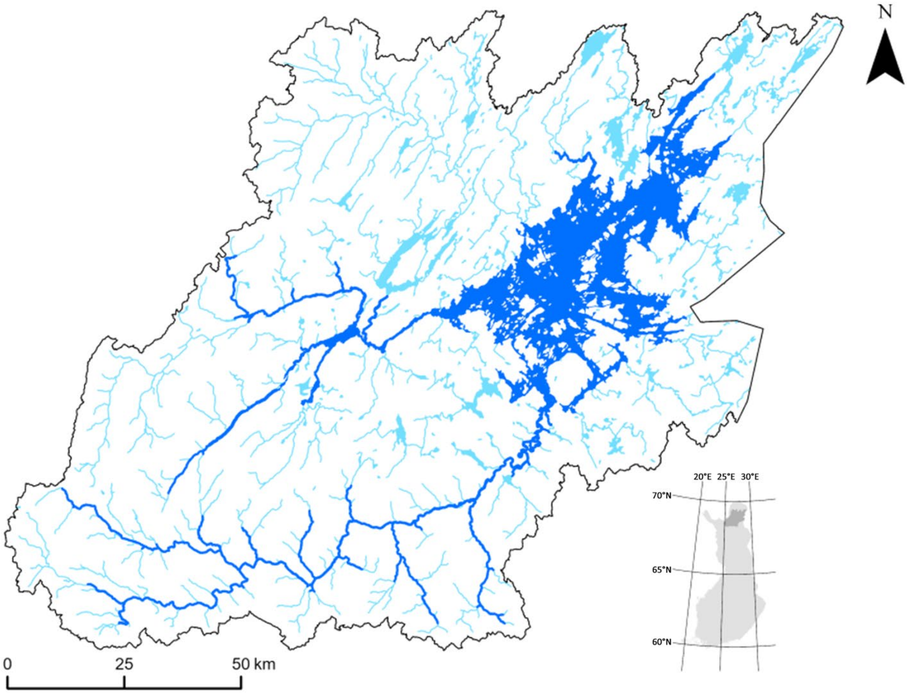

FIGURE 1 | Map of Lake Inari and the surrounding river watercourse. The area covered by the fisheries monitoring programme, which provided the fish samples, is marked in darker blue.

introduced in the mid-1960s, and it subsequently spread widely across the lake, becoming an important component of the lake food web and a key prey species to piscivores (Salonen 2021).

The water level of Lake Inari has been controlled by hydropower dams in Paatsjoki River since the 1940s. To compensate the harm from the hydropower production to the local fisheries, and to augment natural salmonid reproduction, a supplemental stocking programme has been in place since 1975, and the lake fisheries have been monitored since the 1980s. The programme aims to annually release approx. 200,000 1-year-old Arctic charr and 100,000 three-year-old brown trout. Since 2010, stocked fish have accounted for 20%–81% of the annual Arctic charr catch (2.3–9.4 t) and 60%–77% of the annual brown trout catch (14.7–27.3 t) (Natural Resources Institute Finland 2026).

2.2 | Sampling

Fish used in the present study were sampled between 2011 and 2023 in the context of the long-term Lake Inari fisheries monitoring programme. These samples came from local commercial and recreational fishers and were collected throughout the year. Additional brown trout samples came from the two largest rivers inflowing to the lake, Juutua and Ivalo (Figure 1). We hypothesised that the lake's more complex food web and habitat structure would increase parasite burden by providing more transmission opportunities (Blasco-Costa et al. 2013; Karvonen et al. 2015; Paterson et al. 2019), while a high parasite burden may also lower the likelihood of host migration from the lake to the rivers. The fish were obtained either as whole specimens or as partly processed by trained fishers. Partly processed samples included the head and intestines, scales and measurements of total length (at the accuracy of 1 mm) and mass (1 g). Fish had primarily been caught using gillnets, with mesh sizes typically ranging from 40 to 65 mm (bar length measured knot-to-knot), and, to a lesser extent, also by lures and long-lines.

2.3 | Measurements

Researchers or research assistants processed the fish samples at Luke Inari Research Station (68.9° N, 27.0° E). They measured the total length, collected scales and otoliths, weighed body mass, assessed stomach contents by prey species or category (such as coregonids, sticklebacks, benthic macroinvertebrates, insects, unidentified material) and recorded the sex. The main dataset comprised of 1969 Arctic charr (length: 424 ± 121 mm [mean ± SD]; weight: 844 ± 654 g) and 6148 brown trout (length: 507 ± 111 mm; weight: 1617 ± 1101 g) individuals that had complete data for *Dibothriocephalus* count, body condition and origin (stocked/wild, see below). Each sample was also linked to capture metadata (e.g., gear, date, lake/river habitat and sampler ID).

Dibothriocephalus burden was estimated by identifying and counting parasite cysts in the gastrointestinal tract and then recording their numbers using the following categorical scale: 0: no *Dibothriocephalus* detected, 1: 1–10 parasite individuals, 2: 11–30 parasites and 3: >30 parasites. Tapeworm cysts were identified based on their characteristic morphology: pale, round cysts (0.5–1 cm in diameter) located in the fish body cavity, each containing elongated plerocercoids approx. 0.5–4 cm in length. *Dibothriocephalus dendriticum* and *D. ditremus* are the only tapeworm species known to infect the Arctic charr and brown trout in Finland and to form plerocercoid cysts in the body cavity, and, of these, *D. dendriticum* is presumed to be more common (Rahkonen and Koski 1997; Heinimaa and Salonen 2005). In the present study, the two congeneric tapeworm species were not distinguished in the parasite counts, as visual inspection of the cysts is insufficient for species identification. Such identification would require dissection and microscopic examination of each plerocercoid, which was not logistically feasible for the present dataset.

For stomach contents, we used presence versus absence data rather than absolute weight measures in the analyses (see below), because this approach is less sensitive to the measurement procedure and the timing of prey consumption, while providing an indication of whether a given prey category was recently included in the diet.

As a proxy for body condition, we calculated the *scaled mass index* using the total length and body mass data in the *smatr* R package, following the approach of Peig and Green (2009). Briefly, this method estimates the body mass an individual would be expected to have at a fixed reference length (here, the species-specific mean length of the sampled individuals). The index is considered to provide a more robust estimate of body condition than traditional approaches based on, for instance, residuals from body mass—length regressions (Peig and Green 2009). Because Arctic charr and brown trout slightly differ in body shape at a given length, we calculated scaled mass indices separately for the two species. The scaling coefficient that describes the relationship between total length and body mass was 3.298 for Arctic charr and 3.226 for brown trout.

Fish origin (stocked/wild) was identified using the Alizarin Red S (ARS) marking method described by Thorrold et al. (2002). In this method, eggs or juvenile fish are immersed in an ARS solution, which binds to calcified structures, such as otoliths. Stocked fish can subsequently be identified by examining the otoliths under a fluorescence microscope. In the current study, otoliths were extracted and prepared following standard procedures. They were transversely sectioned, polished and then examined under a fluorescence microscope equipped with appropriate excitation and emission filters for ARS detection.

2.4 | Statistical Analyses

All analyses were run using R 4.2.2 software (R Development Core Team). Because of the species differences in body shape, we fitted all analyses that included either total length or scaled mass index (as a proxy for body condition) separately for the two species.

First, to compare parasite burden between the two species, we fitted an ordinal regression model (using the *ordinal* package) with the ordered *Dibothriocephalus* count category (0–3) as the response variable and species (Arctic charr/brown trout) as the sole fixed effect.

Next, to investigate how host stomach contents, traits and origin, as well as temporal aspects, relate to the *Dibothriocephalus* burden, we fitted similar ordinal regression models separately for the two species. Here, fixed effects included the presence of three-spined stickleback or nine-spine stickleback remnants (0/1), the presence of other fish remnants (0/1), the presence of non-fish food items (0/1), total length, body condition (scaled mass index), season (categorical variable with months 3–5 denoted as spring, 6–8 as summer, 9–11 as autumn and 12–2 as winter), year (2011–2023, as an integer variable with 13 possible values) and origin (wild/stocked). In addition, for brown trout, we included habitat as another fixed effect, categorising individuals to those from the lake ($N = 4842$) or from the inflowing rivers ($N = 1306$). This factor was not included in the Arctic charr analysis because only two charr samples were collected in rivers.

To facilitate graphical presentations and comparability to other studies, we repeated all the above analyses with the alteration that we now treated the parasite count category as a count variable. In these models, we fitted Generalised Linear Models (GLMs) with a negative binomial distribution. The two analytical approaches yielded very similar results, and we clearly point out the single case in which they provided a differing conclusion (see Results). Consequently, we were able to use the GLM outputs for graphical illustrations.

Finally, to assess whether parasite burden affected growth, we fitted separate GLMs for the two species, assuming a Gamma distribution. Log-transformed total length was fitted as the response variable. Here, an interaction between age and parasite burden (*Dibothriocephalus* count category) allowed us to estimate the effect of parasite burden on age-specific length, a proxy for growth. We did not assume a normal distribution due to relatively skewed distributions of total lengths. However, analyses under a normality assumption yielded very similar results and identical conclusions.

3 | Results

The proportions of *Dibothriocephalus* infected Arctic charr (1497/1969, 76%) and brown trout (4753/6148, 77%) were very similar, and the species did not significantly differ from each other in parasite count categories (i.e., parasite burden) (Ordinal regression, $\beta \pm \mathrm{SD} = -0.02330 \pm 0.04712$, $z = -0.495$, $p = 0.62$; GLM, $\beta \pm \mathrm{SD} = -0.01292 \pm 0.02269$, $z = -0.565$, $p = 0.57$).

Having stickleback remnants in the stomach was associated with a higher parasite burden in both species (Arctic charr: Ordinal regression, $\beta \pm \mathrm{SD} = 1.299 \pm 0.238$, $z = 5.468$, $p < 0.0001$; brown trout: $\beta \pm \mathrm{SD} = 0.6239 \pm 0.1166$, $z = 5.350$, $p < 0.0001$; Table 1; Figure 2). In contrast, having remnants of other items, whether of other fish (Arctic charr: $\beta \pm \mathrm{SD} = -0.3444 \pm 0.1111$, $z = -3.101$, $p = 0.0019$; brown trout: $\beta \pm \mathrm{SD} = -0.5033 \pm 0.0520$, $z = -9.676$, $p < 0.0001$) or non-fish food particles (Arctic charr: $\beta \pm \mathrm{SD} = -0.7787 \pm 0.2115$, $z = -3.618$, $p = 0.0002$; brown trout: $\beta \pm \mathrm{SD} = -0.3038 \pm 0.0931$, $z = -3.264$, $p = 0.0011$), was associated with a lower parasite burden (Table 1; Figure 2). Note, however, that in Arctic charr, the effect of stomachs containing fish species other than sticklebacks was not statistically significant when parasite count category was treated as a count variable (Table 1; Figure 2).

Larger (longer) Arctic charr (Ordinal regression, $\beta \pm \mathrm{SD} = 0.00988 \pm 0.00047$, $z = 20.80$, $p < 0.0001$) and brown

TABLE 1 | The results of GLM analyses assessing the relationships between the parasite count category (i.e., parasite burden) and effects of interest in Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) from Lake Inari.

	Arctic charr				**Brown trout**			
	β	**SD**	**z**	**p**	**β**	**SD**	**z**	**p**
Stomach: sticklebacks	0.5173	0.1019	5.078	< 0.0001	0.2457	0.05168	4.755	< 0.0001
Stomach: other fish	−0.05679	0.05453	−1.042	0.30	−0.1906	0.0241	−7.907	< 0.0001
Stomach: non-fish	−0.3902	0.1318	−2.961	0.0031	−0.1189	0.0475	−2.501	0.012
Length	0.00340	0.00020	16.64	< 0.0001	0.00285	0.00011	26.52	< 0.0001
Body condition	−0.00055	0.00021	−2.602	0.0093	−0.00046	0.00006	−7.785	< 0.0001
Year	−0.05304	0.00765	−6.929	< 0.0001	−0.03211	0.00315	−10.21	< 0.0001
Origin	0.2848	0.0564	5.504	< 0.0001	0.01228	0.03026	0.406	0.69
Habitat					−0.3756	0.0315	−11.91	< 0.0001
Spring vs. summer	−0.1356	0.0700	−1.938	0.053	0.1992	0.0449	4.436	< 0.0001
Spring vs. autumn	0.1109	0.0680	1.632	0.10	0.06242	0.04697	1.329	0.18
Spring vs. winter	−0.09426	0.07943	−1.187	0.24	−0.1057	0.0558	−1.895	0.058
Summer vs. autumn	0.2464	0.0608	4.054	< 0.0001	−0.1368	0.0268	−5.096	< 0.0001
Summer vs. winter	0.04129	0.0749	0.551	0.58	−0.3049	0.0420	−7.259	< 0.0001
Autumn vs winter	−0.2052	0.0665	−3.086	0.0020	−0.1681	0.0440	−3.823	0.0001

Note: Corresponding ordinal regression results are reported in the text. Body condition was estimated as scaled mass index.

trout ($\beta \pm SD = 0.00857 \pm 0.00027, z = 32.16, p < 0.0001$) had more parasites (Table 1; Figure 3). Similarly, individuals with lower scaled mass index, that is, those in poorer condition, had a higher parasite burden (Arctic charr: $\beta \pm SD = -0.00119 \pm 0.00045$, $z = -2.645$, $p = 0.0082$; brown trout: $\beta \pm SD = -0.00129 \pm 0.00013$, $z = -9.869$, $p < 0.0001$; Table 1; Figure 3). Parasite burden decreased linearly during the study period, 2011–2023 (Arctic charr: $\beta \pm SD = -0.1494 \pm 0.0162$ $z = -9.218$, $p < 0.0001$; brown trout: $\beta \pm SD = -0.09134 \pm 0.00684$, $z = -13.35$, $p < 0.0001$; Table 1; Figure 3).

In Arctic charr, parasite burden was the highest during autumn months and lowest during summer months (Ordinal regression, summer vs. autumn: $\beta \pm SD = 0.6471 \pm 0.1261$, $z = 5.133$,

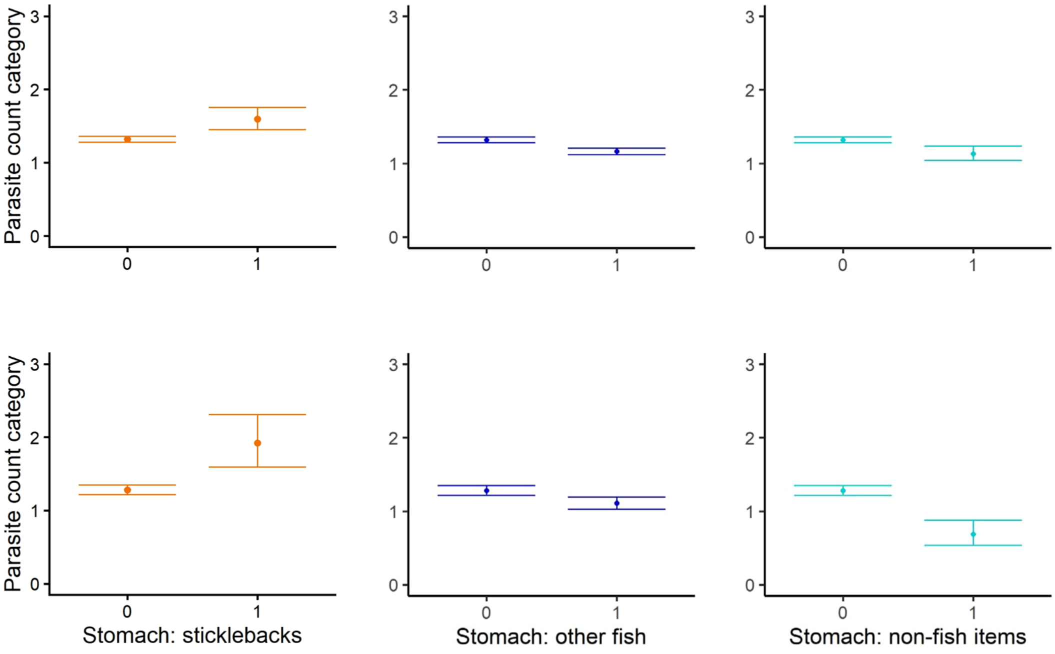

FIGURE 2 | GLM-based illustrations of parasite count category (i.e., parasite burden) in response to presence of different stomach contents in Arctic charr (upper row) and brown trout (lower row). Whiskers indicate 95% confidence intervals. Asterisks indicate statistical significance (*$\alpha = 0.05$, **$\alpha = 0.01$, ***$\alpha = 0.001$). See Table 1 for further details.

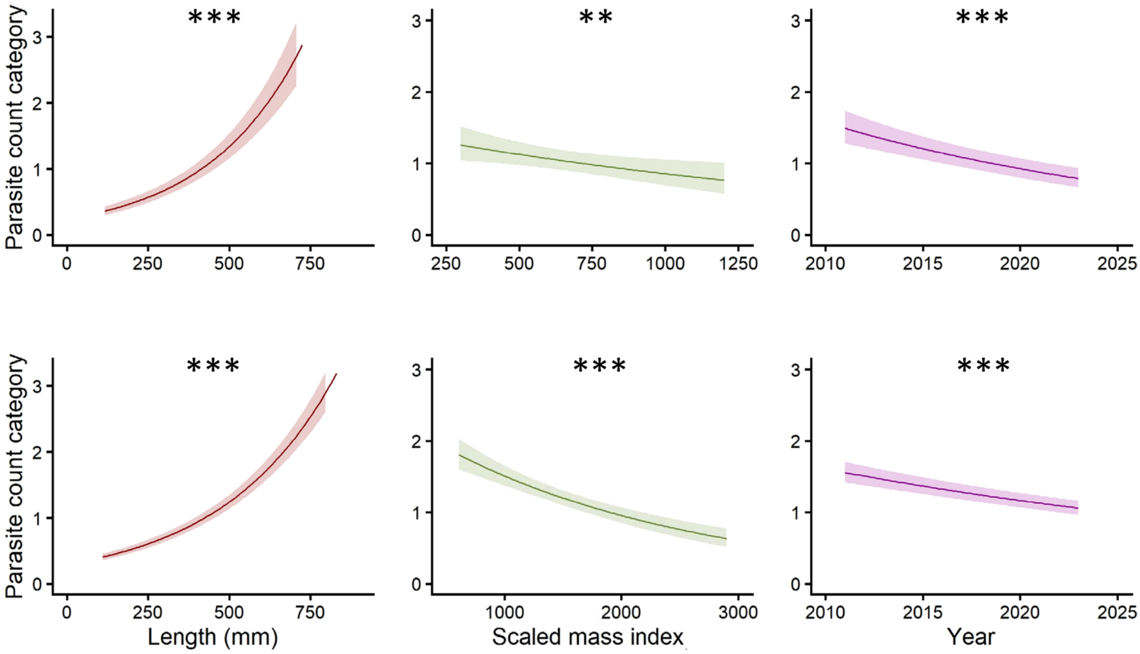

FIGURE 3 | GLM-based illustrations of parasite count category in response to total length, body condition (scaled mass index) and year of sample collection in Arctic charr (upper row) and brown trout (lower row). Shaded areas indicate 95% confidence intervals. Asterisks indicate statistical significance (**$\alpha = 0.01$, ***$\alpha = 0.001$). See Table 1 for further details.

$p < 0.0001$; Table 1; Figure 4), whereas in brown trout, it was the highest during summer months and lowest during winter months (summer vs. winter: $\beta \pm \mathrm{SD} = -0.7822 \pm 0.0867$, $z = -9.021$, $p < 0.0001$; Table 1; Figure 4). In Arctic charr, wild origin was associated with a higher parasite burden ($\beta \pm \mathrm{SD} = 0.8245 \pm 0.1203$, $z = 6.856$, $p < 0.0001$), whereas in brown trout there was no such association ($\beta \pm \mathrm{SD} = -0.04048 \pm 0.06483$, $z = 0.624$, $p = 0.53$; Table 1; Figure 4). Brown trout individuals caught in the lake had a higher parasite burden than individuals from two rivers discharging into the lake ($\beta \pm \mathrm{SD} = -1.102 \pm 0.068$, $z = -16.14$, $p < 0.0001$; Table 1; Figure 4).

The effects of parasite burden and age on length interacted in both species (Arctic charr: GLM, $\beta \pm \mathrm{SD} = -0.00395 \pm 0.00030$, $z = -13.3$, $p < 0.0001$; brown trout: $\beta \pm \mathrm{SD} = -0.00397 \pm 0.00019$, $z = -20.4$, $p < 0.0001$). Specifically, age-specific length (proxy for growth) was smaller with increasing parasite burden (Figure 5).

4 | Discussion

The dominant piscivorous salmonids of Lake Inari, Arctic charr and brown trout, were both commonly infected with *Dibothriocephalus* tapeworms, with the proportion of infected individuals in both species exceeding 70%. Individuals whose stomachs contained fish prey other than sticklebacks, or food items other than fish, exhibited lower *Dibothriocephalus* burdens (as estimated by categories of their counts) compared to individuals lacking these food items. In contrast, larger individuals, those in poorer body condition and those with remnants of three-spined and/or ninespine sticklebacks in their stomach showed, on average, higher *Dibothriocephalus* burdens. Wild (rather than stocked) Arctic charr and brown trout caught in the lake (rather than rivers) were also more heavily parasitised. In both species, individuals with higher parasite burdens had grown more slowly. These findings provide field-based evidence for the importance of trophic interactions in shaping *Dibothriocephalus* infection risk and highlight the key role of sticklebacks in parasite transmission. Furthermore, the results provide evidence for the costs of parasite burden in both salmonids in terms of reduced body condition and growth.

Interestingly, in contrast to other food items, the presence of sticklebacks (three-spined and/or ninespine) in the stomach was associated with higher *Dibothriocephalus* burden. This finding resembles earlier observations that brown trout inhabiting lakes with three-spined sticklebacks were more heavily infected than those in lakes without sticklebacks, likely due to particularly high parasite transmission via this prey species (Kuhn et al. 2016). Together, the previous and current results indicate that sticklebacks have a key role in transmission of tapeworms to subarctic salmonids. In particular, while sticklebacks are commonly consumed by subarctic piscivorous salmonids (L'Abée-Lund et al. 1992; Kuhn et al. 2016; current results), they may more commonly be tapeworm carriers than alternative fish prey (Rahkonen and Koski 1997; Kuhn et al. 2016), presumably owing to their diet and habitat use. More generally, prey availability and abundance (Kahilainen and Lehtonen 2003; Gregersen et al. 2006; Nunn et al. 2012; Hansen and Beauchamp 2014), as well as individual dietary preferences (Reiriz et al. 1998; Nunn et al. 2012; Cirtwill et al. 2016), are likely to influence species and individual level variation in prey consumption. Our results indicate that such prey choices are ultimately linked to parasite burden in these subarctic fish.

We propose two main mechanisms that can explain why more heavily parasitised individuals were in poorer condition and grew slower. First, as previously suggested (Rahkonen and

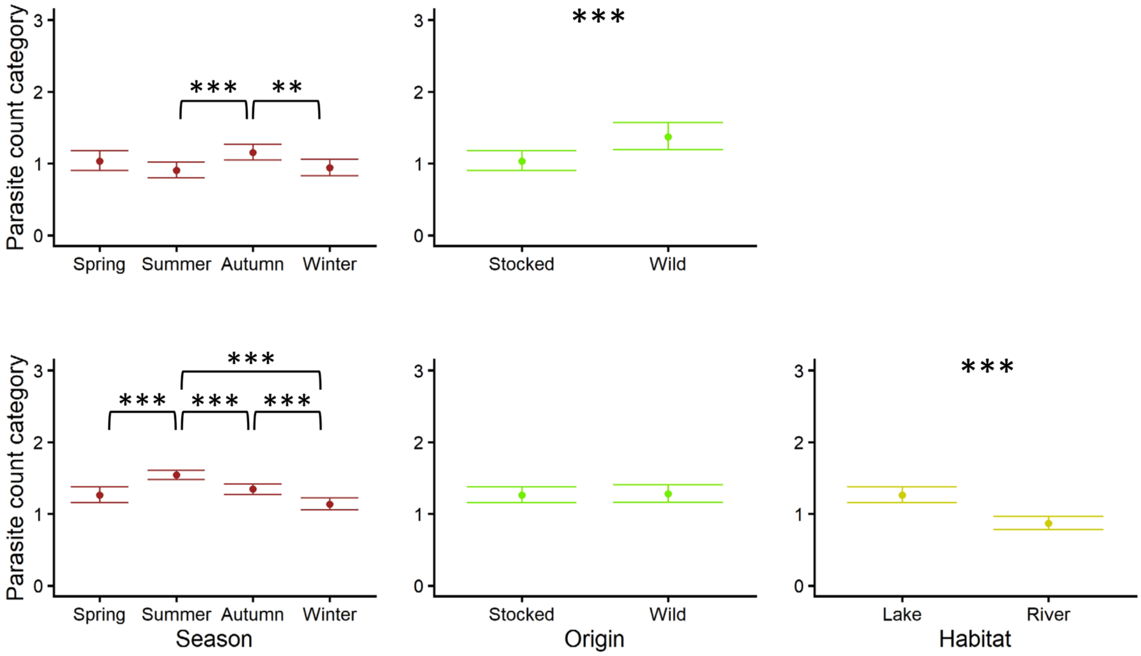

FIGURE 4 | GLM-based illustrations of parasite count category in response to the season and origin in Arctic charr (upper row) and the season, origin and habitat in brown trout (lower row). Shaded areas indicate 95% confidence intervals. Asterisks indicate statistical significance (**$\alpha = 0.01$, ***$\alpha = 0.001$). See Table 1 for further details.

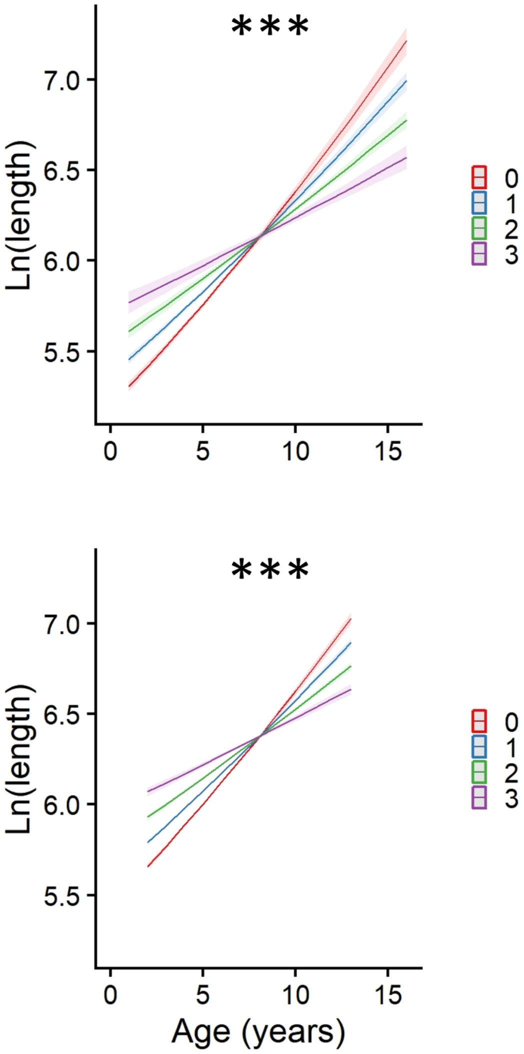

FIGURE 5 | GLM-derived illustrations showing the interactive effects of parasite burden (count categories 0–3) and age (in full years) on length (natural log–transformed), demonstrating parasite-mediated growth in Arctic charr (upper panel) and brown trout (lower panel). Shaded areas represent 95% confidence intervals. Asterisks indicate statistical significance of the interaction effect (***$\alpha = 0.001$).

Koski 1997; Blanar et al. 2005), heavily infected individuals may experience blood loss, nutrient depletion, tissue damage, or secondary infections. These can then lead to reduced vitality and decreased mass relative to body size (here approximated by scaled mass index, a proxy for body condition). Such reductions in body condition may, in turn, negatively affect growth, survival and recruitment (Dutil and Lambert 2000; Armstrong et al. 2018; Korman et al. 2021). The second, non-exclusive explanation for the relationship between parasite burden and body condition is that individuals in better condition or growing quicker may possess stronger immunity, allowing them to accumulate parasites more slowly than those already in poor condition or growing slowly. In a comparable manner, the association between parasite burden and stomach contents other than sticklebacks can have two non-exclusive explanations. Heavily infected individuals may be less capable or driven to capture prey other than sticklebacks, or there is a link between high success when foraging on these prey and robust immunity against parasites. These scenarios are not mutually exclusive, and therefore long-term experimental studies assessing their relative contributions would provide valuable insights and promising avenues for future research.

In addition to the links between parasite burden, diet, condition and growth, parasite burden also increased with body size. *Dibothriocephalus* tapeworms can persist for multiple years, explaining the accumulation over time to larger and older individuals, which is also supported by previous findings on subarctic salmonids (Rahkonen and Koski 1997; Knudsen et al. 2008; Henriksen et al. 2016; Kuhn et al. 2016). Moreover, because Arctic charr and brown trout tend to become increasingly piscivorous as they grow (L'Abée-Lund et al. 1992, L'Abée-Lund et al. 2002; Amundsen 1994; Kahilainen and Lehtonen 2002; Jensen et al. 2015), their exposure to these parasites may increase with the diet change (Henriksen et al. 2016), especially if they increasingly consume sticklebacks. Interestingly, our Lake Inari dataset revealed no significant overall difference in parasite burden between the two species. This result may be somewhat unexpected, given earlier findings of higher *Dibothriocephalus* abundance in charr than in trout in two northern Norwegian lakes (Knudsen et al. 2008) and documented differences in their habitat use, diet and parasite dynamics (Knudsen et al. 2008; Amundsen and Knudsen 2009; Eloranta et al. 2013; Prati et al. 2020). To improve generalisation across systems, we recommend that future studies assessing parasite burden, whenever feasible, use exact parasite counts rather than categorical groupings, which were necessary in the present study due to logistical constraints.

We found that, similarly in both species, *Dibothriocephalus* numbers declined over the study period (2011–2023). This pattern contrasts with earlier suggestions that *Dibothriocephalus* infections in salmonids of subarctic lakes are relatively stable over time (Kuhn et al. 2016). One factor that might contribute to the temporal variation is the proportion of stocked individuals in the population. Specifically, the share of wild Arctic charr in the catches has increased in recent years (Natural Resources Institute Finland 2026), while our data indicate that stocked Arctic charr individuals carried lower parasite burdens, potentially because they spent their early life in a tapeworm-free environment. It is important to note, however, that the temporal decline was significant even when accounting for fish origin in the statistical models. Furthermore, in brown trout, the proportion of stocked individuals in the catches has remained relatively stable (Natural Resources Institute Finland 2026), and we detected no significant difference in parasite burden between stocked and wild brown trout. These findings suggest that factors other than stocking rates, such as changes in environmental conditions, have contributed to the observed temporal trends in parasite burden.

Brown trout caught in rivers had lower parasite burdens than those from the lake, potentially reflecting greater opportunities for parasite transmission within the lake system (Blasco-Costa et al. 2013; Karvonen et al. 2015; Paterson et al. 2019). Furthermore, individuals weakened by a heavy parasite burden may have been less likely to migrate from the lake to the rivers, therefore appearing more commonly in our lake samples. Parasite burden also varied seasonally, with peak levels occurring in autumn (September–November) in Arctic Charr and summer (June–August) in brown trout. Regarding environmental trends over years, there is a growing body of evidence that environmental conditions in Lake Inari have been undergoing notable changes. The lake has been subject to multiple environmental pressures, including temporally variable non-native host species abundances, water level control, increasing water temperatures and changes in winter ice cover (Turunen et al. 2025). In addition, anecdotal reports suggest that the abundance of fish-eating birds (*Larus* and *Mergus* spp.), which serve as final parasite hosts, has declined in the area and prey items other than sticklebacks have become more readily available to the two salmonids (Heinimaa and Salonen 2005; Rytkönen et al. 2015). Many of these changes began prior to the present study period but in some cases have continued and may also have produced lasting carry-over effects on parasite dynamics (Salonen 2021). While climate change may continue to modify fish-parasite interactions further, such trends are challenging to predict, because the combined effects of shifting temperature regimes and parasite exposures remain poorly understood (Casas-Mulet et al. 2021; Lauringson et al. 2021).

To conclude, our results highlight the strong influence of trophic interactions on *Dibothriocephalus* tapeworm burden in Arctic charr and brown trout of Lake Inari. The consumption of stickleback prey played a key role, being associated with higher infection intensity. Despite ecological differences between the two salmonid species, their parasite dynamics were similar. Our findings also highlight costs of *Dibothriocephalus* infection, with higher parasite burdens being associated with reduced body condition and slower growth. Furthermore, parasite burden was associated with wild versus stocked origin in Arctic charr and habitat use in brown trout. We hope that these results will stimulate future experimental research aimed at further unravelling parasite transmission and infection dynamics in subarctic lake ecosystems.

Author Contributions

Topi K. Lehtonen: data curation, formal analysis, visualisation, writing: original draft and writing: review and editing. **Nico Alioravainen:** conceptualisation, data curation, funding acquisition, methodology and writing: review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting this article are available as Supporting Information S1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** The dataset supporting the article. The columns in this Excel file have the following contents: SampleNo = Code that specifies each sample/individual; Habitat = Whether the sample came from Lake Inari or an inflowing river; Species = Arctic charr or brown trout; Length = Total length of the sampled fish (mm); Weight = body mass of the fish (g); ln. length = Natural logarithm of total length; ln. weight = Natural logarithm of weight; ScaledMass = Scaled mass index (proxy for body condition); Sex = 1: Male or 2: Female; Day = Day of the month when the individual was sampled; Month = The month of sampling; Season = Spring (March–May) versus summer (June–August) versus autumn (September–November) versus winter (December–February); Year = The year of sampling; ARScode = Code that identified the Alizarin Red S marking; Origin = Whether the individual was wild or stocked based on the ARS marking; Age = Age of the fish in full years; StomachStickleback = Stomach contents with (1) versus without (0) sticklebacks; StomachOverall = Whether the stomach was empty (0) or with food remnants (1); StomachOtherThanFish = Whether the stomach had food remnants other than fish; StomachFishAll = Identifies stomachs with (1) or without (0) remnants of any fish species; StomachOtherFish = Stomach with (1) or without (0) remnants of other species besides sticklebacks; ParasiteScale = 0: no *Dibothriocephalus* detected, 1: 1–10 parasite individuals detected, 2: 11–30 parasites and 3: > 30 parasites.