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Differences in parasite community composition support ecological differentiation in a freshwater gadoid fish

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Abstract

Several northern freshwater fishes have gone through rapid adaptive radiation after the last glacial period, resulting in new species or intraspecific morphs with distinct life histories. Parasite infections can promote adaptive radiations and spatiotemporal differences in patterns of infections can potentially reveal incipient or ongoing speciation processes. We investigated intraspecific differentiation in a freshwater gadoid fish, burbot (*Lota lota*), by exploring differences in parasite infections between two potential life-history morphs in Lake Konnevesi, Central-Finland, one reproducing species characteristically in shallow littoral waters in February and the other possibly in deep profundal zone roughly a month later. By conducting a sampling campaign on reproducing fish over two consecutive years, we found significant differences in infections between the fish captured from littoral and profundal sites. More specifically, larval trematode and cestode infections were consistently less abundant in profundal fish, tracking long-term exposure differences in shallow waters. In contrast, trophically transmitted metazoan infections in the fish gut, reflecting shorter-term differences in feeding, showed higher variation between sampling years rather than depths. We also found suggestive evidence of higher trematode-inflicted tissue damage per parasite in the profundal fish, implying lower tolerance to the infection. These results offer further evidence that burbot captured from littoral and profundal sites represent differentiated life-history morphs. We propose that ecological and evolutionary differentiation within burbot populations across its circumpolar distribution may be more widespread than previously acknowledged.

KEYWORDS

adaptive radiation, ecotype, eye fluke, gadoid fish, host–parasite interactions, speciation

1 | INTRODUCTION

Several northern freshwater fish species have undergone adaptive radiations after the last glacial period, which in some instances has

resulted in sympatric or parapatric ecotypes or morphs with variable degrees of reproductive isolation (Schluter, 1996; Seehausen & Wagner, 2014; Skúlason et al., 1999). Examples include species such as Arctic charr (Gíslason et al., 1999; Knudsen et al., 2006),

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three-spine stickleback (Matthews et al., 2010; Taylor & McPhail, 2000) and whitefish (Bernatchez et al., 1996; Siwertsson et al., 2010), which represent hallmark examples of rapid speciation processes. However, the range of fish and other aquatic animal taxa potentially in the early stages of ecological differentiation or speciation is probably still underestimated (April et al., 2011; Struck et al., 2018). Species with intraspecific variation in ecological features such as niche occupation or reproductive strategies that have received less attention could include cases of unexplored biodiversity. Thus, research on less-studied fish taxa, in addition to the already well-described systems, is needed for a better understanding of aquatic biodiversity across northern latitudes.

Parasite infections can be used to track differentiating ecological features among potential host ecotypes. Typically, parasitism is spatially and temporally variable because of aggregation of infected hosts or infective stages (Byers et al., 2008; Jokela & Lively, 1995; Jousimo et al., 2014), and seasonality in parasite transmission (Karvonen et al., 2004a; Soubeyrand et al., 2009; Taskinen et al., 1994). Consequently, host individuals and populations showing incipient or advanced polymorphism in life-history characteristics may become differentially exposed to infections. Studies demonstrating differences in parasite infections of freshwater fishes, mostly among well-defined ecotypes or morphs, have been accumulating over the past years (Blais et al., 2007; Eizaguirre et al., 2011; Hablutzel et al., 2016; Karvonen et al., 2013, 2015, 2018; Knudsen et al., 1997, 2003; Maan et al., 2008; MacColl, 2009; Natsopoulou et al., 2012; Raeymaekers et al., 2013), illustrating how parasite infections can reveal differentiation among hosts. Furthermore, infections from parasite taxa with different modes of transmission can reflect different aspects of host ecology. For example, infections that have a relatively short lifespan, such as those of many trophically-transmitted adult intestinal parasites (Karvonen et al., 2005; Valtonen, 1979; Valtonen et al., 1984), can provide important information on differences in recent feeding behaviour. On the other hand, longer-lasting infections, such as those that accumulate in fish over years (Burrough, 1978; Dieterich & Eckmann, 2000; Marcogliese et al., 2001; Pulkkinen & Valtonen, 1999), can reveal other forms of differentiation like habitat use. Thus, differences in infections that are consistent or track host exposure over a long period of time can be useful for detecting signals of early ecological differentiation among hosts.

By definition, parasites cause harm to their hosts, which is why hosts often counter adverse effects with costly defences (Lochmiller & Deerenberg, 2000; Sheldon & Verhulst, 1996). Over time, differences in rates of infections that reduce host fitness can result in divergence in the ability of populations to resist infections. For example, by comparing immune responses of river and lake ecotypes of three-spined sticklebacks, Kalbe and Kurtz (2006) demonstrated lower immunological responses in the river ecotypes that experience lower infection from a common trematode parasite. Similarly, major histocompatibility complex genotypes of sticklebacks are known to become locally adapted to population-specific parasites, indicating that selection is acting to promote divergence in genes that confer immunity in lake and river populations (Eizaguirre et al., 2012a). Such differences in infection pressure also could potentially

underlie variation in other defence components, that is the ability to tolerate (e.g. repair damages) or avoid infections (e.g. moving away from the source of infection), which can be complementary to resistance or traded-off with it (Klemme et al., 2020; Medzhitov et al., 2012; Råberg et al., 2009; Read et al., 2008).

Here, we studied parasite infections of burbot (*Lota lota*), a circumpolar freshwater gadoid fish with a relatively poorly known ecology compared with many other freshwater fish species. In Northern Europe, burbot is known to reproduce in shallow (typically 0.5–1.5 m) waters in mid-winter (Lehtonen, 1998). Offspring hatch at break-up of ice in the following spring and spend the first 2–3 years of life in littoral areas feeding on aquatic invertebrates and small fish (Eloranta, 1982; Mills & Eloranta, 1985). Older burbot move to deep cool waters and return to shallow areas in late autumn (Lehtonen, 1998). After spawning they move again to deep waters (>10–15 m in depth). In contrast, in Lake Constance, at the southern edges of their distribution, burbot spawn in the profundal zone at depths of more than 40 m (Probst, 2008), sometimes even as late as the end of May (Fischer, 1999). Studies in the Great Lakes of North America have also shown that burbot can have genetically differentiated subpopulations within one lake, with some populations reproducing in shallow littoral waters in winter, while others spawn in deep profundal waters in spring and summer (Blumstein et al., 2018; Elmer et al., 2008; Jude et al., 2013; Underwood et al., 2016). However, intrapopulation differences are unlikely to be limited to these particular lake systems. Rather, intraspecific differentiation is probably more common given the circumpolar distribution of burbot across large lakes, where suitable conditions for different reproductive strategies, for example along the spatial littoral–profundal and temporal continuums, are likely to be met.

We studied parasitism in burbot inhabiting Lake Konnevesi in Central Finland, where fish appear to exhibit polymorphic features (Marjomäki et al., 2022): some individuals spawn in littoral areas in February (hereafter “littoral burbot”), but mature ripe individuals can also be found in profundal depths of >30 m roughly one month later (“profundal burbot”). Actual spawning in the profundal zone, however, is yet to be verified. In addition to spawning time, there is some evidence of differentiation in morphology and feeding ecology: profundal burbot have higher somatic body weight, slower growth, wider head and lower $\delta^{13}\text{C}$ isotope values compared to littoral burbot (Marjomäki et al., 2022). Parasite infections provide yet another means to track ecological features of differentiating fish populations, including habitat use and diet (Karvonen et al., 2013, 2018; Knudsen et al., 1996; MacColl, 2009; Raeymaekers et al., 2013). We were particularly interested in differences in infections of (1) long-lived larval trematodes and cestodes, which infect juvenile burbot in shallow waters during the summer months and (2) trophically transmitted adult metazoans in the intestine, which have a shorter lifespan. Following the ontogenetic habitat shift of burbot, long-lived parasite infections acquired in the littoral zone during the summer months should remain in fish for years. Thus, if the potential littoral and profundal-spawning ecotypes of burbot showed differences in ontogeny in shallow waters, we would expect differences in infections of these

TABLE 1 Developmental stages, sites of infection and mean abundances (\pm SE) of the parasite taxa observed in littoral and profundal burbot (*Lota lota*) in Lake Konnevesi, Central Finland, in 2019 and 2020

| Parasite taxa | Developmental stage | Site of infection | Littoral | | Profundal | |
|--------------------------------|-----------------------|-------------------|----------------|----------------|----------------|-----------------|
| | | | 2019 (n = 5) | 2020 (n = 30) | 2019 (n = 20) | 2020 (n = 10) |
| <i>Diplostomum</i> spp. | Larval trematode | Eye lens | 38.3 \pm 5.4 | 26.4 \pm 4.3 | 5.1 \pm 1.6 | 7.2 \pm 1.1 |
| <i>Diplostomum</i> spp. | Larval trematode | Eye humour | 49.6 \pm 5.4 | 40.3 \pm 8.2 | 14.3 \pm 2.5 | 15.4 \pm 3.3 |
| <i>Tyloodelphys</i> sp. | Larval trematode | Eye humour | 1.6 \pm 0.7 | 0.1 \pm 0.1 | 0 | 0.3 \pm 0.2 |
| <i>Triaenophorus nodulosus</i> | Larval cestode | Liver | 8.4 \pm 3.0 | 13.8 \pm 2.1 | 5.8 \pm 1.4 | 4.3 \pm 1.1 |
| <i>Eubothrium rugosum</i> | Adult cestode | Intestine | 0.2 \pm 0.2 | 1.3 \pm 0.3 | 0.7 \pm 0.2 | 1.3 \pm 0.5 |
| <i>Proteocephalus</i> sp. | Adult cestode | Intestine | 0.2 \pm 0.2 | 2.5 \pm 0.8 | 0.3 \pm 0.2 | 0.6 \pm 0.3 |
| Unidentified nematodes | Adult nematodes | Intestine | 3.4 \pm 1.4 | 44.7 \pm 7.9 | 11.7 \pm 3.5 | 57.7 \pm 12.1 |
| <i>Acanthocephalus lucii</i> | Adult acanthocephalan | Intestine | 0 | 4.8 \pm 2.0 | 2.5 \pm 0.7 | 0 |
| <i>Echinorhynchus borealis</i> | Adult acanthocephalan | Intestine | 0.6 \pm 0.4 | 25.6 \pm 9.9 | 12.5 \pm 3.2 | 17.9 \pm 6.2 |

parasites. Similarly, potential differences in the feeding ecology of adult fish could be expected to result in consistent differences in their intestinal parasite fauna.

2 | MATERIALS AND METHODS

2.1 | Sampling design

In total, 65 burbot with a representative size range (194–585 mm) were retrieved from fyke nets of a commercial fisherman. Individuals included in the samples were selected visually to evenly capture the length distribution of the catch. Samples were collected from previously characterised littoral (1–1.5 m) and profundal (ca. 30 m) sites, located approximately 1 km apart within the same basin of Lake Konnevesi, Central-Finland, in 2019 and 2020 (sites L1 and P1 in Marjomäki et al. (2022)). Sampling on reproducing fish was conducted in the littoral site in mid-February and in the profundal site in mid-March in both years. However, due to poor ice conditions in February 2019, the littoral sample in that year was taken from a different location, but the profundal samples originated from the same location in both years. Fish were euthanized by the fisherman immediately after being caught and transferred to the laboratory on ice. Each fish was measured for total length (mm) and characterised for sex (length ranges (min-max) were 255–509 and 194–585 mm for littoral and 269–551 and 337–498 mm for profundal burbot, in 2019 and 2020 respectively). It was also determined, based on the developmental stage of the gonads, that all fish were ready to spawn or already spawning at the time of sampling.

2.2 | Parasitological examination

Before dissection for parasite infections, the eye lenses of each fish were examined for parasitic cataracts caused by *Diplostomum*

spp. trematodes using a slit-lamp microscope (Kowa SL-15). Cataracts have notable fitness consequences for fish (Karvonen, 2012), and the intensity of cataracts can be used in interpreting differences in tolerance between fish populations (Klemme et al., 2020). Here, the intensity of cataracts was scored as 0%–100% with 10% increments (Karvonen et al., 2004b). The eye lenses and humour were then dissected separately, and all larval trematodes (long-lived metacercarial stages) in each tissue were counted under a microscope. Subsequently, the liver was removed from each fish and dissected and examined under a microscope for cysts of the trophically transmitted cestode *Triaenophorus nodulosus* (long-lived larval stage). Similarly, the intestine was removed, opened and examined for infections of trophically transmitted cestodes, nematodes and acanthocephalans (shorter-lived adult stages).

2.3 | Data analysis

Data on parasite abundances were analysed using GLMs with negative binomial probability distribution and log-link function. Sampling depth (littoral/profundal), year (2019/2020) and sex (male/female) were used as fixed factors and fish length as a covariate. Similarly, differences in cataract intensities were analysed using GLM and the same fixed variables. To interpret possible differences between the littoral and profundal burbot in tolerance to parasite-inflicted damage, the relationship between $\ln(y+1)$ -transformed cataract intensity and $\ln(x+1)$ -transformed abundance of the lens-infecting *Diplostomum* spp. was analysed using GLM (normal probability distribution and identity-link function) with sampling depth (littoral/profundal, years combined) as a fixed factor and parasite abundance as a continuous variable. Since no cataracts were observed among the uninfected eyes and all infected eyes had at least some cataracts, the relationships were forced through the origin, following Klemme et al. (2020). All analyses were conducted in SPSS 26.

3 | RESULTS

For both sampling years, total abundance of larval *Diplostomum* eye flukes was significantly higher in littoral burbot compared with profundal burbot (GLM: Wald $\chi^2 = 17.140$, $p < .001$ (depth), $\chi^2 = 0.039$, $p = 0.844$ (year), $\chi^2 = 0.495$, $p = .482$ (depth \times year); Table 1, Figure 1a), although the latter included one clearly deviating individual with 84 *Diplostomum* parasites. The results were similar when tested separately for the lens-infecting (effect of depth: $\chi^2 = 26.189$, $p < .001$) and humour-infecting ($\chi^2 = 12.136$, $p < .001$) species of *Diplostomum*. The long-lived trophically transmitted larval cestode, *Triaenophorus nodulosus*, infecting the liver of burbot, showed a similar pattern on infection according to depth ($\chi^2 = 5.377$, $p = .020$; Table 1). The effect of fish length on abundance of these parasites was not significant in any of the GLMs ($p > .63$ for all).

Abundances of the shorter-lived adult intestinal parasites exhibited more variation between sampling years. In the full model, total abundances of these parasites were higher in 2020 compared to 2019 in littoral burbot but only marginally so in profundal burbot (GLM: $\chi^2 = 7.810$, $p = .005$ (depth \times year); Table 1, Figure 1b). However, pairwise tests separately examining sampling depths found that there were higher abundances in 2020 in both littoral ($\chi^2 = 28.603$, $p < .001$) and profundal burbot ($\chi^2 = 6.945$, $p = .008$). The observed patterns were driven mainly by the acanthocephalan *Echinorhynchus borealis* (effect of year, depths combined: $\chi^2 = 10.470$, $p = .001$) and unidentified nematodes ($\chi^2 = 35.347$, $p < .001$) that accounted for 33% and 60% of all intestinal infections respectively (Table 1). Fish length, considered as a covariate, was not significant ($p = .996$). The main effect of fish sex, and interactions between sex and the other variables, were not significant in any of the above tests ($p > .16$ for all) and therefore fish sex was left out of the final models.

Infections of *Diplostomum* spp. in the eye lenses resulted in parasite-induced cataracts and the intensity of cataracts (mean for right and left eye of each fish) was higher in the littoral burbot compared to profundal fish (GLM: $\chi^2 = 5.601$, $p = .018$ (depth), $\chi^2 = 0.133$, $p = .716$ (year), $\chi^2 = 0.365$, $p = .546$ (depth \times year)). The slope of the relationship between *Diplostomum* abundance and cataract intensity was significantly steeper for profundal burbot compared to littoral fish (GLM: $\chi^2 = 18.827$, $p < .001$ (depth \times *Diplostomum* abundance; Figure 2)), suggesting that profundal burbot had a higher intensity of cataracts at a given parasite abundance.

4 | DISCUSSION

Parasite infections can be used to track habitat use and diet preferences of differentiating fish populations (Karvonen et al., 2013, 2018; Knudsen et al., 1996; MacColl, 2009; Raeymaekers et al., 2013). The nature and extent of intraspecific variation within freshwater fishes is probably still unknown, particularly in less-studied species, which can result in underestimation of biological diversity. We investigated parasite community composition of burbot to explore if infections differed between potential littoral and profundal-spawning

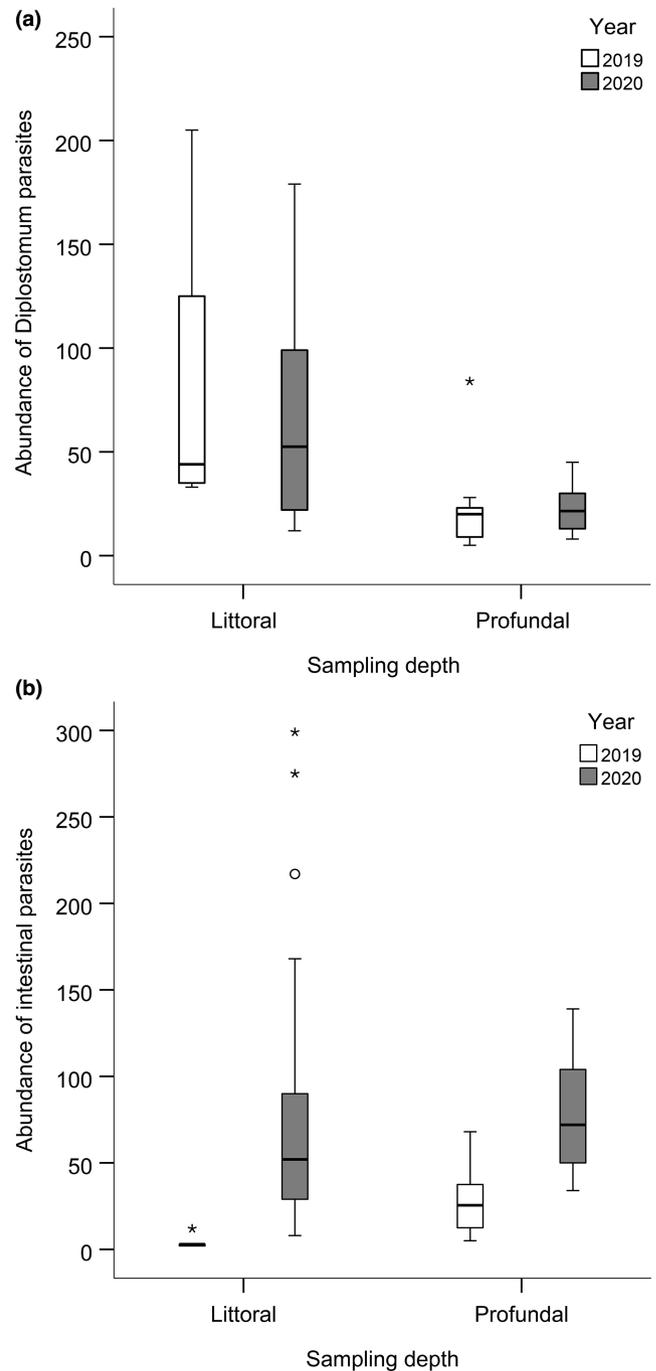


FIGURE 1 Abundance of *Diplostomum* spp. trematodes in the eyes (a) and trophically transmitted cestode, nematode and acanthocephalan infections in the intestine (b) of burbot (*Lota lota*) captured from littoral (shallow) and profundal (deep) areas of Lake Konnevesi during the spawning season in 2019 and 2020. Circles indicate outlier values and asterisks show extreme values

life-history morphs. We found that the communities differed significantly between the littoral and profundal fish, particularly in infections from larval trematodes and cestodes that accumulate in fish over years. In contrast, adult intestinal parasites that have a shorter lifespan exhibited greater variation between sampling years than depths. Furthermore, profundal burbot seemed to have a

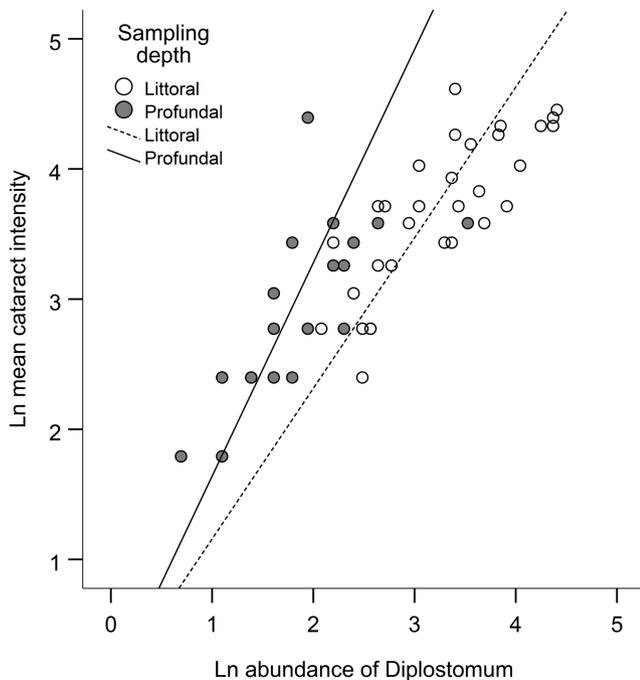


FIGURE 2 Relationships between abundance of *Diplostomum* spp. and corresponding intensity of parasite-induced cataracts in the eye lenses of burbot (*Lota lota*) captured from littoral (open circles) and profundal (filled circles) areas of Lake Konnevesi during the spawning season in winter 2019 and 2020 (years combined). The fitted lines indicate slopes of the relationships through the origin for littoral (dashed line) and profundal (solid line) burbot

lower tolerance to parasite-inflicted eye damage. Overall, these results suggest long-term differences in infections, providing further evidence of ecological and possibly evolutionary differentiation between burbot sub-populations within a single lake.

Lower abundances of eye flukes and larval cestodes in profundal burbot suggest they experience lower exposure to these parasites compared with littoral fish. The eye-infecting larval trematodes transmit to fish from snail intermediate hosts in shallow waters during summer months (Chappell et al., 1994; Karvonen et al., 2004a). Similarly, the larval cestode *T. nodulosus* transmits to fish in littoral areas, following the release of parasite eggs from the pike (*Esox lucius*) definitive host and infection of the first intermediate copepod host in early summer (Kuperman, 1981). Consequently, transmission is concentrated to shallow waters and there is likely to be very little or no transmission of these parasites in deeper areas, where adult burbot are typically found after the mid-winter spawning until next autumn (Lehtonen, 1998). This suggests that possible exposure differences take place when young burbot live in littoral areas (Eloranta, 1982; Mills & Eloranta, 1985) and overlap spatially with the parasite intermediate hosts. This is supported also by the non-significant effect of fish length on parasite abundances in this study, suggesting that parasite abundances do not increase with size (age) in adult fishes.

While the details of the reproductive behaviour and ontogeny of potential burbot ecotypes in the study area are unknown, these

data suggest that profundal burbot spend less time in shallow waters when young compared with littoral burbot. This could be because of their later arrival to shallow areas following possible hatching in deeper waters and a pelagic larval stage, occupation of deeper parts of the littoral zone or earlier departure from shallow areas compared with littoral fish. Interestingly, in Lake Constance, where burbot spawn in deep profundal waters, the larvae are pelagic (Fischer, 1999) and the juvenile littoral phase ends at a length of about 12 cm, when the fish are presumably about one year old (Fischer & Eckmann, 1997). In Konnevesi, 2–3-year-old individuals also have been found in the littoral zone (Mills & Eloranta, 1985). Our data on parasite infections thus suggest that the juvenile profundal burbot may behave more similarly to those in Lake Constance. Currently, it is unknown if the littoral-hatching burbot larvae in Konnevesi visit the pelagic zone or whether they remain exclusively in the littoral zone. However, burbot larvae have been routinely caught in pelagic larval sampling of Finnish lakes (Karjalainen et al., 1998). It should be noted that in addition to exposure, the ecotypes could also differ in susceptibility to infections, for example if variation in infection risk has favoured divergence in resistance profiles (Eizaguirre et al., 2012b). However, aspects of immunological responses to infections are currently unknown.

We also detected that most of the adult intestinal parasites exhibited greater variation between sampling years rather than depths. The parasite communities of both littoral and profundal fish were dominated by nematodes and the acanthocephalan *E. borealis*, the latter being transmitted to burbot via the benthic crustacean *Pallasea quadrispinosa* found in deep lake basins (Tuomainen et al., 2015). Thus, the spatial overlap of adult burbot and the parasite's intermediate host is the likely reason for the observed similar patterns of infections in littoral and profundal fish. However, infections differed significantly between the sampling years. This is probably partly explained by the different littoral sampling location in 2019, but the higher abundances in deeper water habitat suggest higher parasite transmission in 2020 overall. In general, spatiotemporal variation in parasitism is a predominant feature in aquatic host-parasite systems (Byers et al., 2008; Faltýnková et al., 2008; Jokela & Lively, 1995), including acanthocephalans (Karvonen et al., 2005; Valtonen, 1979), which can be explained, for example by population dynamics of the intermediate hosts. Consequently, differences in these shorter term infections support annual variation rather than consistency between the sub-populations, although stable isotope analyses have suggested at least some differences in feeding ecology between littoral and profundal burbot (Marjomäki et al., 2022).

We also found some evidence of higher eye lens damage per parasite in the profundal burbot although, overall, the littoral fish suffered more from cataracts because of higher parasite abundance. This result is suggestive of lower tolerance in the profundal fish to *Diplostomum*-induced cataracts (Klemme et al., 2020). In general, these parasites and cataracts they cause can influence fish phenotype and behaviour in many different ways (Karvonen, 2012). For example, it has been shown that the parasites reduce feeding efficiency and growth of infected fish (Crowden & Broom,

1980; Karvonen & Seppälä, 2008) and also make the fish more susceptible to predation (Seppälä et al., 2005). However, these effects are likely to be host species-specific, and it is currently unclear to what extent burbot suffer from potential effects of infections. Effects on susceptibility to predation are most likely to occur during early years of life when burbot acquire infections in the littoral zone (see above) and are prone to predation from fish-eating birds and predatory fish. The risk of avian predation is subsequently reduced as the burbot grow and move to deeper waters, although the risk of increased fish predation among heavily infected individuals can remain. Moreover, adult burbot are unlikely to significantly suffer from reduced vision in deeper darker waters, where they can rely on other senses to find food and potential mates. In Konnevesi, the littoral-caught burbot typically grow faster than the profundal-caught individuals (Marjomäki et al., 2022), but it is unknown to what extent parasite infections contribute to the differences in growth rate.

The indication of lower tolerance among the profundal fish further supports the inference that littoral and profundal burbot in Lake Konnevesi may represent differentiated ecotypes. It is possible that lower parasite exposure among profundal fish has favoured lower investment into defences such as tolerance. However, it should be noted that our sample sizes and the overlap in cataract distributions between the littoral and profundal fish were relatively small. Moreover, tolerance should also be investigated in relation to resistance because of possible interactions between the defence components (Klemme et al., 2020), but such analysis was not possible from the current data. Thus, our results on tolerance differences should be considered approximate and interpreted with caution. It is also possible that the fish samples taken from the profundal site in March may have contained both littoral and profundal fish as the littoral-spawning fish typically return to deeper (>10–15 m) waters after spawning (Lehtonen, 1998). However, there was only one individual caught from the profundal site that resembled a littoral fish in numbers of larval parasites, which suggests that any large-scale mixing had not yet occurred.

To conclude, differences between the littoral and profundal burbot in infections of the accumulating larval parasites and in their ability to tolerate these infections suggests ecological and possibly evolutionary differentiation between ecotypes in Lake Konnevesi. Considered alongside evidence of ecotypes in North America, these data suggest broader, previously unknown biological diversity in this gadoid fish species. The high number of systems across the circum-polar distribution of burbot, where conditions for similar differentiation are likely to be met, suggests a high probability of further cases to be described in future investigations. Along with other ecological and genetic methods, examining parasitism can potentially shed new light on differentiation across other populations of burbot.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to study design and data collection. AK analysed the data and drafted the first version of the manuscript with input from all authors. All authors gave approval to the final draft and submission.

DATA AVAILABILITY STATEMENT

Original data are available in JYX Digital Repository of the University of Jyväskylä: <https://doi.org/10.17011/jyx/dataset/80574>.

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