UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Stability and recovery of parasite communities in dynamic host environments

Assessing the impact of host behaviour, environmental changes, and anthropogenic disturbances on parasitic communities

Eloïse Coralie Rochat

A dissertation for the degree of Philosophiae Doctor (PhD) August 2024

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The hidden world of Parasites

The host is an island invaded by strangers with different needs, different food requirements, different localities which to raise their progeny – Taliaferro.

Cover Image

The cover images were generated using DALL E artificial intelligence. I asked for picture showing Arctic charr in Norwegian lake that transition into fjord in the back to illustrate the landscape were my three studies take place.

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Acknowledgments

Firstly, I want to thank my three supervisors: Rune Knudsen, Isabel Blasco Costa and Rachel Paterson, for their support and guidance through the last four years. It has been a privilege to learn from such dedicated and knowledgeable mentors. Thank you, Rune, for your enthusiasm and for sharing your widespread knowledge of ecology and freshwater and for your optimistic view on everything. For being welcoming and supportive when I moved to Tromsø. Isa, I am grateful to you who has been an exceptional mentor and guide from my master's thesis to the completion of my PhD. Your support and advice have been an important for my academic development. Thank you for your everlasting care and concern for all your students. Rachel, thank you for your dedication and passion for science that have been truly inspiring. Our discussions on ecology and parasitology have greatly enriched my knowledge and my approach to research. I am deeply appreciative of the time you have invested in sharing your expertise and insights, which have invaluable contributions to my scientific journey. Thank you, for your significant impact on my academic and personal growth.

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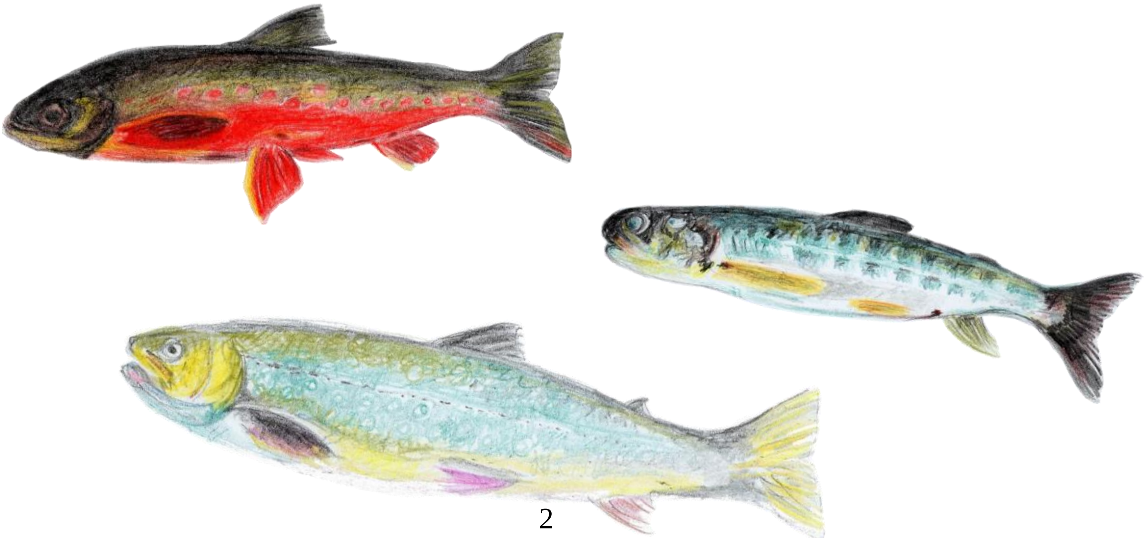

© Arctic charr by my mum, Nathalie Follonier

Summary

This thesis provides an investigation of the stability and recovery of parasite communities within dynamic ecological environments, focusing particularly on the host-parasite interactions in aquatic ecosystems. Arctic charr (*Salvelinus alpinus* L), a European salmonid, with its diverse morphological forms and broad ecological niches, provides a unique lens through which to examine the interactions between hosts and parasites and their collective response to environmental changes.

The first study within the thesis, **Paper I**, examines how interventions such as the restocking of species and the introduction of non-native species influence the parasite communities of polymorphic hosts. The findings indicate that despite significant shifts in the fish community, parasite communities within different morphs of Arctic charr demonstrated remarkable stability over time. This indicates a resilient adaptation of parasites to host dynamics and environmental changes. Then, **Paper II** focuses on the response of parasite communities to the eradication of fish hosts in two Norwegian lakes. This part of the research reveals that following the drastic ecological disturbance of host eradication, parasite communities exhibited an ability to recover and re-establish close to their pre-disturbance diversity and structure. This recovery underscores the inherent resilience within ecological systems and suggests that parasite communities possess dynamic recovery mechanisms enabling them to rebound from population disruptions. Finally, **Paper III** assesses the influence of seasonal migration on the parasitic load in anadromous hosts. This study shows parasite communities are richer and more abundant in migratory individuals compared to their non-migratory counterparts. This suggests that migration introduces higher recruitment of parasites, potentially influencing the fitness and survival strategies of the host species. Moreover, the parasite communities showed stability in both freshwater and marine ecosystems.

Overall, this thesis contributes to the field of parasitological and ecological research by showing that parasite communities can be stable and recover when faced with environmental and host changes. These helminths communities in freshwater fish have maintained their structure and functionality despite significant disturbances, such as restocking, species introductions, eradication, and natural host migrations.

List of papers

Paper I

Rochat, E. C., Paterson, R. A., Blasco-Costa, I., Power, M., Adams, C. E., Greer, R. and Knudsen, R. (2022). Temporal stability of polymorphic Arctic charr parasite communities reflects sustained divergent trophic niches. Ecology and Evolution, **12**, e9460.

Paper II

Rochat E.C., Blasco-Costa I., Hansen H., Poulin R., Selbach C., Knudsen R. and Paterson R.A. (2024) “Parasite community re-assembly following eradication: is it predictable?” (advanced manuscript)

Paper III

Rochat E.C., Auestad Nilsen H., Grenier G., Selbach C., Knudsen R., Blasco-Costa I. and Rachel A. Paterson (2024) “Assessing parasite communities in anadromous Arctic charr: is it a cost of migration?” (advanced manuscript)

Authors contribution

	Paper I	**Paper II**	**Paper III**
Concept and idea	RK, RAP, IB, MP, ER, CA	RAP, ER, RK, IB, RP, HH	ER, RK
Study design and methods	RK, RAP, IB, CA, MP, ER	ER, RK, HH, RP, RAP	ER, RK, IB, RAP
Data gathering and interpretation	RK, IB, ER, CA, RG, RAP	ER, RK, IB, RAP, RP, CS	ER, RK, IB, CS, RAP
Manuscript preparation	ER, RK, IB, RAP, MP, CA	ER, RK, IB, CS, RAP, RP, HH	ER, RK, IB, CS, RAP, GG, HN

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Introduction

Ecosystems are intricate networks where each component, from the smallest microorganisms to the largest predators, plays a critical role in maintaining biodiversity and ecological health (e.g. Hooper *et al.*, 2005; Hartmann & Six, 2023). Ecological studies have long attempted to unravel the complex web of interactions that define ecosystems. Traditionally, scientists have often focused on distinct elements (e.g. a species of interest) within these systems, analysing them in isolation to understand their individual roles. However, this compartmentalization belies the interconnectedness inherent in Earth's biodiversity (e.g. Bascompte & Jordano, 2007; Su *et al.*, 2023). Across various ecosystems, a complex network not only facilitates the exchange of nutrients, organisms, and energy but also underpins the functioning and resilience of these systems. Among these movements, the migrations of animals have been extensively studied (Chapman *et al.*, 2014), yet the movement of parasites that live in or on these hosts remains a critically overlooked aspect (e.g. Poulin & Morand, 2000; Poulin, 2007; Timi & Poulin, 2020). These often-neglected organisms, which are as numerous and diverse as free-living species (Poulin, 1997; Lymbery & Smit, 2023), play significant roles in ecological and evolutionary processes and exert major selective pressures on their hosts by living at their expenses (Marcogliese, 2004; Poulin, 2021). The intricate relationship between hosts and parasites across landscapes reveals much about the mechanisms that govern the functioning and stability of the ecosystem (Marcogliese, 2005; Hudson *et al.*, 2006).

1 Parasite communities

Parasites, despite their negative connotations, play a role in regulating populations and maintaining biodiversity (Thomas *et al.*, 1999; Hudson *et al.*, 2006). Parasites help control the population size of their hosts, preventing overgrowth and ensuring resource availability by infecting and sometimes killing their hosts (e.g. Anderson & May, 1979; Tompkins *et al.*, 2011; Rózsa & Garay, 2023). Moreover, the interactions between parasites and hosts are complex, creating a dynamic network that influences the fitness and behaviour of both parties (e.g. Moore, 2002; Poulin, 2010). Parasite communities (Box 1), are influenced by host interaction within the ecosystem network, representing a complex aspect of ecological research (Altizer *et al.*, 2011; VanderWaal & Ezenwa, 2016). Movements driven by natural behaviours or anthropogenic factors significantly affect the distribution, transmission, and diversity of parasites (e.g. Bradley & Altizer, 2007; Lafferty, 2012; Altizer *et al.*, 2013). Understanding these dynamics is essential not only for elucidating the fundamental mechanisms of parasite transmission but also for developing effective management strategies for parasite burdens in wildlife populations, which in turn impacts conservation initiatives (Rubio-Godoy & de León, 2023).

Box 1: Parasite community terminology

Parasite community terminology refers to the specialized language used to describe the diverse interactions between parasites and their hosts within ecosystems (Kennedy, 1990; Bush *et al.*, 1997). This terminology encompasses terms that denote the composition, structure, and dynamics of parasite communities, including parameters such as **richness** (the number of parasite species infecting a host individual or population), **abundance** (the number of individual parasites within a host), **prevalence** (the proportion of hosts infected with a particular parasite), and **intensity** (the average numbers of parasites per infected host). The parasite **infracommunity** refers to the parasites found within a single individual host. In other words, it represents the collection of all parasite species inhabiting a particular host organism at a given point in time. For example, if a fish is infected with three different types of parasites (e.g., a fluke, a tapeworm, and a nematode), the collection of these parasites within that individual fish represents its infracommunity. Then, the parasite **component community** refers to the entire array of parasite species found in all individuals of one host population within a defined geographical area or ecosystem. In essence, it is the sum of the total of parasite species infecting all individuals of a particular host species within a specific habitat. For instance, if we were to examine a population of fish in a lake and find that collectively they harbour five different parasite species, the combination of these parasites across all the fish in the lake represents the component community for that host population.

Parasite communities prosper in dynamic environments, where the continuous flux of host movements shapes their structure and diversity (e.g. Lafferty & Kuris, 2002; VanderWaal & Ezenwa, 2016). These movements, whether part of natural migratory patterns or driven by anthropogenic changes such as habitat fragmentation and climate shifts, introduce parasites to new hosts and environments, facilitating the spread and evolution of these parasites (e.g. Altizer *et al.*, 2013). The adaptation of parasite and host communities to changing environmental conditions is an attestation to their possible stability and resilience (e.g. Dunn *et al.*, 2012;

Carlson *et al.*, 2017; Lanfranchi *et al.*, 2024). As hosts cross different ecosystems, they carry with them a suite of parasites, which in turn can affect local parasite populations by introducing new pathogenic strains or species, potentially leading to changes in local disease dynamics (e.g. Kelly *et al.*, 2009; Tompkins *et al.*, 2011; Donaldson *et al.*, 2024). Furthermore, the stability of parasite communities is important to ensure that parasite loads remain within manageable levels, reducing the risk of host morbidity and mortality (Anderson & May, 1978; Hudson *et al.*, 2006). Hosts with high but stable parasite communities are better able to allocate resources to growth, reproduction, and other essential functions (e.g. Møller & Saino, 1994). The stability of parasite communities in relation to changes in host populations through time and space is a pivotal aspect of ecological research, reflecting the dynamic interplay between organisms and their environments (e.g. Ostfeld & Keesing, 2000; Dobson *et al.*, 2008; Lanfranchi *et al.*, 2024). Additionally, stable parasite communities contribute to overall ecosystem biodiversity, supporting the persistence of diverse host populations and maintaining ecosystem resilience to environmental changes (e.g. Thomas *et al.*, 1999; Dunn *et al.*, 2009). The composition and structure of parasite communities can also change significantly, as host populations increase, disperse, or undergo fluctuations due to environmental pressures or human activities (e.g. Nunn *et al.*, 2003; Johnson & Hoverman, 2012). These shifts are not merely incidental but are indicative of broader ecological processes, including resilience, and the flow of energy through ecosystems (Loreau & De Mazancourt, 2013).

While many studies emphasize the adaptability and resilience of parasite communities in dynamic environments, some researchers suggest the instability of parasite communities (e.g. Lafferty & Kuris, 1999; Alizon & van Baalen, 2008). These studies argue that parasite communities are susceptible to fluctuations in host populations, environmental changes, and anthropogenic disturbances, which can lead to significant shifts in parasite diversity and abundance (e.g. Marcogliese, 2023). For instance, alterations in land use, climate variability, and host migration patterns are frequently cited as factors that can disrupt established parasite-host interactions, potentially leading to the loss of parasite species or the emergence of new host-parasitic relationships (e.g. Grenfell & Dobson, 1995; Dobson & Foufopoulos, 2001). This perspective highlights the fragility of parasite communities, suggesting that their stability is often overstated and that they may be among the first indicators of ecological distress (e.g. Poulin, 1992; Thieltges *et al.*, 2013; Lanfranchi *et al.*, 2024). Such insights challenge the notion of resilience and adaptability, instead underscoring the vulnerability of parasite communities to rapid and often unpredictable environmental transformations.

However, the overall impact on parasite community structure and diversity of host local ecological changes (i.e. host restocking), host removal and migration are not well characterized in aquatic ecosystems (e.g. Sarabeev *et al.*, 2022; Marcogliese, 2023). For instance, how does introducing a new species (intentionally or unintentionally) alter the balance of parasite species within an ecosystem? Similarly, how does eradicating a species affect the parasite community, particularly in terms of parasite load, community structure, or diversity? How fast can parasite community re-establishes or recover following disturbances? So far, long-term studies on the temporal dynamics of parasite communities in response to ecological condition changes are rare. Understanding how parasite communities respond to temporal and spatial changes in host populations provides crucial insights into ecosystem structure and stability (e.g. Lafferty *et al.*, 2006; Hechinger *et al.*, 2011). This knowledge would allow us to better predict potential disruptions and devise strategies that ensure the sustainability of these complex biological networks (Marcogliese, 2005). Indeed, the resilience of parasite communities would show despite disturbance on the system, the communities can recover and maintain its stability (Gunderson, 2000). Thus, comprehending how parasite communities develop over time following an introduction, eradication, or natural migration event is crucial for predicting long-term impacts on ecosystem dynamics. Indeed, while restocking and species introductions can bring new hosts and parasites into an ecosystem (e.g. Kelly *et al.*, 2009; Simberloff, 2009; Peeler *et al.*, 2011), how they might affect the complex dynamics of native parasite communities is often poorly understood.

2 Why aquatic ecosystems?

Aquatic ecosystems including freshwater and coastal ecosystems are the main focal environments of this thesis. Freshwater ecosystems are among the most dynamic and threatened habitats worldwide (Strayer & Dudgeon, 2010) and support approximately 6% of the planet’s biodiversity (Dudgeon *et al.*, 2006). They are the arenas where the impact of human activity (i.e. such as pollution, habitat alteration, species introduction, and climate change) is most intensely felt (e.g. Nilsson *et al.*, 2005; Palmer *et al.*, 2010; Woodward *et al.*, 2010). These pressures not only disrupt the lives of conspicuous species but also alter the hidden connections mediated by parasites, which play essential roles in regulating host populations and maintaining ecosystem health (e.g. Poulin, 2006; Sures, 2008). Environmental disturbances, whether natural or human-induced, pose significant threats to these ecosystems, affecting not only the hosts but also their parasitic counterparts (e.g. Dušek *et al.*, 1998; Mouritsen *et al.*, 2018). Although the notion of parasite extinction might appear beneficial from a human-centric viewpoint, it ignores the crucial roles these organisms play in nutrient and energy flows within wildlife and ecosystems (Wood & Johnson, 2015).

The pronounced seasonality typical of northern freshwater ecosystems adds complexity to the ecological dynamics in these regions, subjecting aquatic species to prominent seasonal shifts that can magnify the impact of environmental changes on their life cycles and interactions with parasites (e.g. Mouritsen & Poulin, 2002; Altizer *et al.*, 2006; Karvonen *et al.*, 2013). These seasonal variations are critical in understanding how host-parasite relationships adapt and respond to changing environmental conditions (e.g. Michalakis & Hochberg, 1994; Lafferty & Kuris, 1999). Arctic charr, *Salvelinus alpinus* L., serves as an exemplary model for studying host-parasite interactions within freshwater ecosystems. These fish are ecologically significant due to their high latitude distribution and varied life history strategies over the seasons, which include multiple morphs coexisting within a single lake (see Box 2 and Prati *et al.* (2020)). This diversity makes Arctic charr an ideal subject for examining how environmental changes affect species interactions and ecosystem (e.g. Klemetsen *et al.*, 2003; Reist *et al.*, 2006).

Box 2: Model system - Arctic charr

Arctic charr (*Salvelinus alpinus* L.) is a species of freshwater fish native to cold, northern regions, including Arctic and sub-Arctic areas. Renowned for their resilience and adaptability, Arctic charrs thrive in diverse habitats ranging from high mountain lakes to coastal marine environments (e.g. anadromous population migrating between two habitats). They exhibit a remarkable array of morphological and behavioural adaptations that allow them to survive in harsh conditions, such as their ability to tolerate low oxygen levels and their capacity to withstand cold temperatures (Nordeng, 1983; Klemetsen *et al.*, 2003). Where sympatric morphs of Arctic charrs co-exist, they typically segregate based on their trophic niche, often with a minimum of one morph that feeds in the benthic environment and one morph that relies more heavily on food available in the water column (Walker *et al.*, 1988; Skúlason *et al.*, 1989; Adams, 1998; Skoglund *et al.*, 2015). These different morphotypes can live and reproduce together within a lake (Adams, 1998) but they also can be genetically segregated populations within a waterbody (Adams, 1998; Præbel *et al.*, 2016) and show a high conservation value (Fraser & Adams, 1997). Arctic charrs display considerable variation in colouration, with individuals ranging from silver to dark brown, often exhibiting distinctive markings. Their diet typically consists of a variety of prey, including aquatic invertebrates, small fish, and zooplankton (Walker *et al.*, 1988; Adams *et al.*, 2003; Smalås *et al.*, 2013; Simonsen *et al.*, 2017; Moccetti *et al.*, 2019). Moreover, Arctic charrs harbour an array of parasites, reflecting their wide-ranging habitat and varied diet (Frandsen *et al.*, 1989; Knudsen *et al.*, 1997; Amundsen *et al.*, 2009). Arctic charrs host several parasite taxa (cestodes, trematodes, nematodes, acanthocephalans) which are trophically transmitted to the host through the predation of intermediate hosts (Moravec, 2004).

Changes in aquatic ecosystems, particularly those driven by anthropogenic activities and climate changes, have already substantially altered these systems across broad geographic regions, especially in northern latitudes (e.g. Harley *et al.*, 2006; Woodward *et al.*, 2010; Hayden *et al.*, 2019). The ongoing and future anthropogenic disturbances threaten biodiversity and the functional integrity of aquatic ecosystems (e.g. Christensen *et al.*, 2006; Harley *et al.*, 2006; Ficke *et al.*, 2007; Tylianakis *et al.*, 2008; Jackson *et al.*, 2016). Thus, understanding the responses of ecosystems to such changes, particularly through the lens of complex parasite life cycles that span multiple trophic levels, is imperative. Parasites, as indicators of environmental change and integral components of food webs (Lanfranchi *et al.*, 2024), provide invaluable models for studying ecosystem resilience and the cascading effects of disturbances across trophic interactions.

3 Significance of the thesis

This thesis contributes to filling knowledge gaps in our understanding of how dynamic environmental changes influence parasite communities within aquatic ecosystems. Despite the critical roles that parasites play in ecological and evolutionary processes, there remains a substantial deficit in comprehensive studies that examine the stability and resilience of these communities in response to disturbances such as climate change, and anthropogenic impacts. Moreover, the relationships between parasite dynamics and host migratory behaviours are not well understood, particularly how these behaviours affect the stability and resilience of parasite communities. By addressing these critical gaps, this thesis will offer deeper insights into the intricate interdependencies within ecosystems and improve our knowledge in predicting and managing ecological responses to global changes. Overall, this research seeks to contribute to ecological theory by providing a better understanding of parasite-host dynamics and their adaptations to environmental shifts. It would also help in predicting how disturbances will affect ecological networks, which is vital for sustaining fisheries and preserving freshwater biodiversity. Furthermore, the studies of the parasite communities have the novelty to be based on parasite species identification.

Thesis objectives and research questions

The present PhD thesis aim is to analyse the stability and recovery of complex parasite communities in hosts populations in dynamic environments over time. The three **papers** included in the thesis strategically addresses central gaps in our knowledge about how parasite communities are shaped by ecological changes, eradication, and migration of their host population (see Figure 1).

First, the main aim of **Paper I** is to evaluate the temporal stability of parasite communities in response to local anthropogenic ecological changes such as the restocking and introduction of new species. Specifically, it aims at the understanding of how parasite communities are affected by translocated species. Additionally, the study examines whether distinct parasite communities of three polymorphic hosts, feeding on the main preys that are suitable for trophic transmitted parasite taxa, with different ecological niches stay stable through time. The research also explores the indirect effects of introduced fish species on parasite communities, considering changes in predator-prey relationships and resource competition.

Second, **Paper II** aims at assessing whether parasite community' structure and diversity can recover their original condition after removal of host populations. It seeks to gain understanding of the recruitment and re-establishment mechanisms of parasites within host populations, specifically after a mass eradication. This field experiment compares the long-term development of parasite communities in a host species (pre- and post-data) across disturbed (two treated lakes) and undisturbed (control) lake environments.

Third, **Paper III** investigates the parasite community' structure across two different habitats through host migration. It seeks to understand how parasite communities change in relationship with their host's seasonal migration patterns and feeding behaviours. By comparing the parasite diversity and abundance between migratory and non-migratory host individuals and examining the consistency of parasite communities over two successive migration cycles, the study provides valuable insights into how migration impacts parasite dynamics in host populations.

Collectively, these studies show the importance of considering parasites in ecological and conservation management frameworks. By detailing how parasite dynamics respond to host behaviour, community changes, and anthropogenic impacts, this thesis increases our understanding of ecological communities in changing environments. It contributes to our broader understanding of how ecosystems function and recovery, providing valuable insights for managing biodiversity and ecosystem state in a changing world.

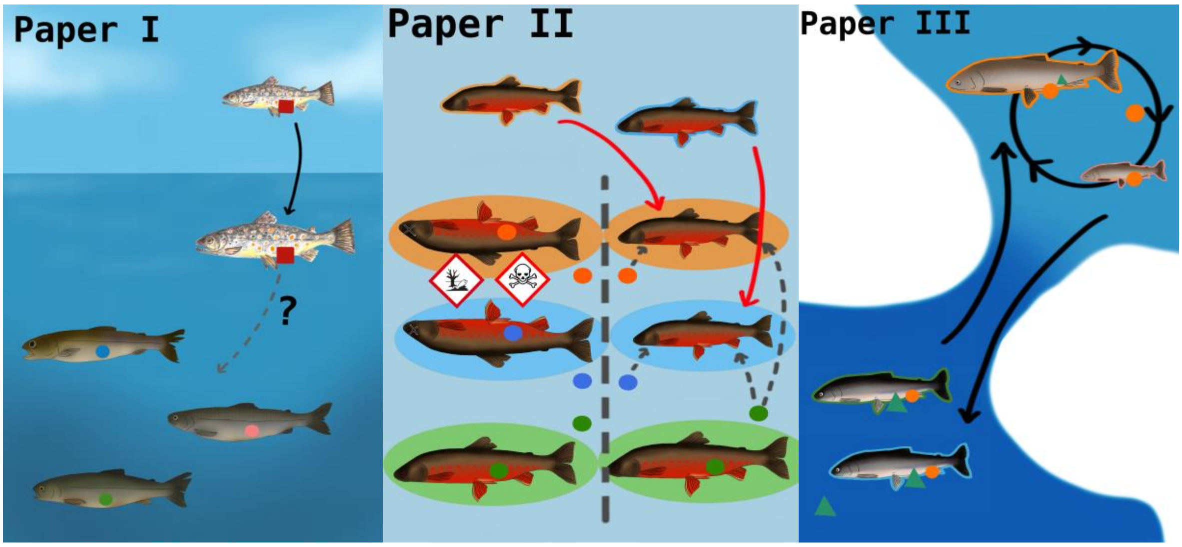

Figure 1: Graphical representation of the thesis goals. Paper I assessed the effect of fish restocking on the parasite communities of three morphs of Arctic charr (green—benthivore morph; blue—piscivore morph; and pink—planktivore morph). Paper II examines at the re-establishment and re-assembly process of parasites in host communities after a large-scale eradication event (two treated lakes: orange – Fustvatnet, blue – Ømmervatnet and one untreated lake: green – Luktvatnet). Finally, Paper III examined the influence of marine migration on the parasite community in anadromous Arctic charr using pre-migrants (pink), migrants (green – 2020 and blue – 2021) and post-migrants (orange). The dots correspond to the freshwater parasite infecting Arctic charr, in Arctic charr or in their intermediate host. The triangle shapes represent the marine parasite infecting Arctic charr, in charr or in their intermediate host. Then, the square shapes are the parasite community of sympatric fish (e.g. brown trout). The tick arrow represents the fish movement, and the dashed arrow indicate the parasites' movement. Fish drawing made by Nicole Rochat.

Methodology

This thesis explores the parasite infracommunity of European Arctic charr (*Salvelinus alpinus* L.) in three papers each with distinctive methodological approaches. The following descriptions of the methods are broad to avoid redundancies with the individual papers; further details and specifications can be found in the respective papers. Overall, Arctic charr parasite community of a total of five lakes were studied in this work.

1 Study systems

Arctic charr populations studied in the thesis were in the United Kingdom (**Paper I**) and Norway (**Paper II** and **III**). One of the populations was situated in Scotland, four were in northern Norway in Nordland and Troms County.

The first paper of this thesis investigates the parasite community of Arctic charr from Loch Rannoch, Scotland (Figure 2). Loch Rannoch is an oligotrophic lake in the Tayside Region, Scottish Highlands (Bryce *et al.*, 2016; Rochat *et al.*, 2022). The Arctic charr population in Loch Rannoch comprises three morphs (a littoral benthivore, planktivore and profundal piscivore morph, see Figure 2 and Adams *et al.* (1998)), which differ in terms of their functional trophic morphologies (Adams & Huntingford, 2002; Bryce *et al.*, 2016), life-history traits (Adams & Huntingford, 2004; Fraser *et al.*, 2008), trophic niches (Adams *et al.*, 1998) and parasites (Dorucu, 1996).

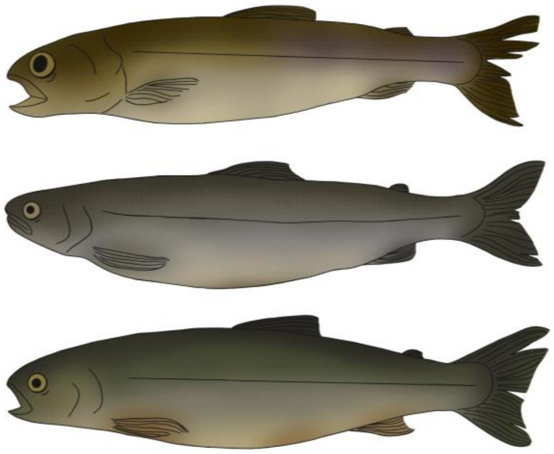

Figure 2: Arctic charr from Loch Rannoch, from the top to bottom, piscivorous, planktivorous and benthivorous. Drawing made by Nicole Rochat

The second paper follows the work of Paterson *et al.* (2018) on parasite distribution in Arctic charr populations from the Fusta catchment in Norway. The Fusta catchment (544 km^2), Nordland County, northern Norway comprises a series of linearly connected oligotrophic lakes: Luktvatnet, Ømmervatnet, Mjåvatnet and Fustvatnet that are connected to the Vefsn fjord by the Fusta river (Paterson *et al.*, 2018). Before 2012, the fish communities in this catchment were composed of landlocked Arctic charr, landlocked & anadromous brown trout *Salmo trutta* L., threespined stickleback *Gasterosteus aculeatus* L. in addition of a few European eel *Anguilla anguilla* L. and Atlantic salmon *Salmon salar* L. (Sæter, 1995; Paterson *et al.*, 2018).

After the discovery of *Gyrodactylus salaris* (Malmberg, 1957), an invasive parasite (see Box 3), in the Fusta catchment, Ømmervatnet, Mjåvatnet and Fustvatnet were treated using rotenone treatment in Autumn 2012 (Hanssen, 2013). Treatment resulted in the removal of all the fish in the lakes, and subsequent cascading effects on the other taxa due to the absence of keystone predators (Kjærstad *et al.*, 2022). Native Arctic charr and brown trout, bred in a fish hatchery in 2012, were reintroduced to the lakes in late 2013 and spring 2014, allowing us to study the parasite community re-establishment.

Box 3: Rotenone treatment against *Gyrodactylus salaris*

Rotenone treatment has been a significant method employed by authorities in Norway to combat the invasive parasite *Gyrodactylus salaris*, which poses a severe threat to native salmonid populations (Adolfsen *et al.*, 2021). *Gyrodactylus salaris*, a parasitic flatworm, introduced during the 1970s in Norway, has the potential to devastate salmonid populations by causing extensive mortality among juvenile fish (up to 98% mortality rate, Johnsen *et al.*, 1999). Multiple treatments were tested in laboratory or field (e.g. Poléo *et al.*, 2004) and the most successful was the use of the plant-derived poison rotenone (Guttvik *et al.*, 2004). Rotenone is used to eradicate the parasite by selectively targeting and killing fish populations in infested rivers and water bodies (Guttvik *et al.*, 2004). The treatment involves the careful application of rotenone to affected areas, effectively eliminating both fish and their parasite, such as salmonid fry. Although rotenone treatment can be highly effective in eradicating *Gyrodactylus salaris* from specific water systems, its use is subject to strict regulations and environmental assessments due to its potential impact on non-target species and ecosystems. Nonetheless, in cases where alternative control methods have proven ineffective, rotenone treatment remains a crucial tool in the ongoing efforts to protect Norway's native salmonid populations from the devastating effects of *Gyrodactylus salaris* infestations. Nowadays, the use of rotenone to combat *Gyrodactylus salaris* remains controversial due to its environmental implications (Bardal, 2019). Increasing concerns over biodiversity and ecosystem health have led to stricter regulations and a push for more sustainable alternatives (e.g. use of hyperparasites or predators Woo & Buchmann, 2012). Consequently, recent strategies involve an integrated pest management approach that includes biological control measures, habitat restoration, and improved surveillance and diagnostic techniques (Sitjà-Bobadilla & Oidtmann, 2017).

Paper III focuses on the parasite community in the anadromous Arctic charr from Laksvatnet in a northern lake-fjord system (Balsfjord), 50 km southeast of Tromsø. The lake's surface area is 0.8 km^2 with a river stretch of 600 meters before entering the relatively pristine Balsfjord (salmon farms are not allowed in this fjord). This lake is mainly inhabited by a population of anadromous Arctic charr, but the lake also holds sea trout (*Salmo trutta* L.) and sporadically Atlantic salmon (*Salmo salar* L.) (Svenning *et al.*, 2013). The project follows the anadromous Arctic charr population over two years (Figure 3). The 2-year data is included in a study of anadromous Arctic charr populations in Balsfjord under the leadership of Dr. Hallvard Jensen (NIBIO) and in collaboration with other institutions (NiNord and the Inland Norway University).

Figure 3: Anadromous Arctic charr from Laksvatnet sampled on their way back from the sea (on the top) and in the lake (on the bottom). Photograph by Eloïse Rochat.

2 Sampling methods

The thesis used a combination of available long-term parasite data collected between 1992 and 2019 as well as samples collected specifically for this thesis projects. **Papers I** and **II** utilized datasets from Dorucu *et al.* (1995), (1996) and Paterson *et al.* (2018). The anadromous Arctic charr used in **Paper III** were all dissected during this thesis.

A combination of nets was used to sample the fish from the various habitats in the lakes. Gill nets were deployed overnight in Loch Rannoch for a maximum period of 12 hours during

October 1992, July 1993 and October 2010 (see Dorucu *et al.*, 1995). Multi-mesh gillnets were used to ensure a random sample and to allow for the calculation of catch per unit effort (**Paper II** and **III**). Over the years multi-mesh gillnets have consisted of both survey nets and Nordic nets (see the papers for the nets details and placements). Nets were typically set overnight and retrieved in the morning. Sixty fish (**Paper II**) were collected in 2012 during the rotenone treatment in Fustvatnet and Ømmervatnet (data used in Paterson *et al.*, 2018). Anadromous individuals from **Paper III** were sampled during their migration returning to Laksvatn in the Buktelva River in 2020 with a fish trap (see trap description in Grenier, 2023).

All fish collected were frozen for later laboratory examination. The dissections were performed in a standardized manner. Arctic charr were weighed (g) and measured (fork length, mm) as a standard first step (Klemetsen *et al.*, 1997; Smalås *et al.*, 2013; Knudsen *et al.*, 2019; Moccetti *et al.*, 2019). The sagittal otoliths were removed and preserved in alcohol for age determination. The stomachs were removed and assessed to assign a degree of fullness (0 to 100%) before being preserved in ethanol for stomach content analysis (Amundsen *et al.*, 2008). Preserved stomachs were dissected in the laboratory (**Paper I**) and contents were identified to estimate their contribution to the fullness estimate (Amundsen, 1994). Gonads were examined for sex determination and assigned a stage of maturity (Klemetsen *et al.*, 1997; Smalås *et al.*, 2013). A muscle sample was excised from the muscle tissue above the lateral line, in between the dorsal fin and caudal peduncle, and frozen (Moccetti *et al.*, 2019).

3 Parasitological examination

Fish were thawed and dissected under a stereomicroscope and all the organs and tissues were examined for metazoan parasites. The parasites collected during the organ dissections were morphologically identified to species or genera using morphological criteria (e.g. Moravec, 2004) before specimens were fixed in absolute ethanol for molecular analyses. I selected some of the specimens used for the morphological analyses and rehydrated them, as preservation in absolute ethanol shrinks and/or modifies the internal structures of the worms. I prepared whole mounts according to protocols by Cribb and Bray (2010) and Justine *et al.* (2012). Molecular data were acquired from a subset of specimens representing each potential parasite taxon to validate their morphological identification. The DNA extraction, PCR amplification of the large ribosomal subunit (28S rDNA) and small ribosomal subunit (18S rDNA), sequencing analysis and phylogenetic analysis were carried out as described in **Paper I** (Rochat *et al.*, 2022), **Paper II** and **Paper III**.

4 Diet and isotopic analyses

Stomach contents collected from the upper end of the oesophagus to the pyloric sphincter (for **Paper I**) were identified to the lowest practical taxonomic level (typically order or family) under a stereomicroscope. The frequency of occurrence of each prey category was evaluated as volume percentage for each stomach and each food category (Hyslop, 1980). Dorsal muscle tissue samples from Arctic charr sampled in Loch Rannoch and Laksvatnet were prepared following a standardised method as described in **Paper I** (Rochat *et al.*, 2022), and Grenier (2023).

5 Statistical approaches

The infection parameters such as parasite prevalence and mean abundance (see Box 1) were calculated for each parasite species (Bush *et al.*, 1997). All analyses were carried out on the parasite component and infracommunities of Arctic charr and performed with the statistical software R version 3.004 (www.r-project.org). My datasets included information on fish (age, sex, length and weight) for each sampling, in addition to the parasite species and their abundance in each fish.

The diversity of parasites at the infrapopulation level was evaluated and analysed using various methods. Generalized linear models (GLM) were used to analyse differences in species richness, diversity, and parasite abundances across lakes and years (see **Paper I** and **III**). These models were fitted with suitable Poisson or quasi-Poisson distributions to accommodate over-dispersion identified by dispersion tests *AER::dispersiontest* (Kleiber & Zeileis, 2008). The dissimilarity among parasite infracommunities over time, as a function of the lake or habitat, were evaluated using the multidimensional scaling ordination method (MDS) with Bray Curtis distance matrix (Oksanen, 2015). The significance of predictor variables (lakes and years) and their interaction was tested with a permutational multivariate analysis of variance (PERMANOVA) as detailed in each paper methods.

Additionally for **Paper II**, three other analysis were performed. The distribution and abundance of various parasite species within the Arctic charr host population, between the lakes, and within each lake, were concurrently analysed using Joint Species Distribution Modeling (JSDM) with *mvabund* package (Wang *et al.*, 2012). This statistical approach is ideal for examining the relationships between species, environmental covariates, and treatment effects as explained in **Paper II** methods. Furthermore, differences in parasite prevalence and mean abundances over time were evaluated in each lake with a Chi-square test for all species at the component community level. Subsequently, the variation in the commonness and rareness of parasite species was analysed over time in each lake. The data were sorted, and the probability of each species being common was computed with confidence intervals using the functions from the *FuzziQ* package (Balbuena *et al.*, 2021).

Summary of the Results

1 Summary of results from Paper I

Temporal stability of polymorphic Arctic charr parasite communities reflects sustained divergent trophic niches

In this study, the parasite communities in Arctic charr before and after local ecological changes, i.e. restocking of a host, were compared to assess the temporal stability of parasite communities in three host morphotypes.

The study on Arctic charr revealed morph-specific differences in stomach contents, parasite communities, and stable isotope values through time (Figure 4). Planktivore morphs showed the highest proportion of empty stomachs (39.3%) and low stomach fullness, contrasting with benthivore morphs with only 5.7% empty stomachs and 54.2% stomach fullness. Piscivore morphs displayed intermediate values. Diet varied among morphs, with high fish consumption by piscivores, and high chironomid larvae consumption by benthivores and planktivores.

Stable isotope analysis revealed morph-specific differences in $\delta^{15}N$ values, indicating dietary variations. Piscivores had higher $\delta^{15}N$ values, reflecting a fish-based diet, while benthivores had the lowest values. Planktivores and benthivores had the highest probabilities of sharing the same trophic region. The study highlighted temporal stability in the polymorphic Arctic charr population.

Eleven parasite taxa were found in 2010, including four new ones. The total parasite prevalence increased between 1992-93 and 2010, with 100% prevalence in piscivores and planktivores, and 88.2% in benthivores. Piscivores had higher overall parasite abundance than benthivores, which, in turn, had a higher abundance than planktivores. Parasite species composition differed between morphs, with distinct patterns in infection. Parasite infracommunities also showed morph-specific segregation and stability over time, making up for the over stability of the Arctic charr morph stability.

Main conclusions

Paper I revealed that despite variations in the broader fish community due to stocking and species introductions, Arctic charr morphs maintained distinct and stable diet and therefore trophically transmitted parasite profiles. Piscivores, with a diet rich in fish, showed higher parasite prevalence and abundance. In contrast, planktivores often had empty stomachs and lower fullness, indicating less consistent access to food resources, while benthivores primarily consumed chironomid larvae and showed moderate parasite levels. The temporal stability observed underscores the adaptability and resilience of Arctic charr morphs to environmental and anthropogenic changes.

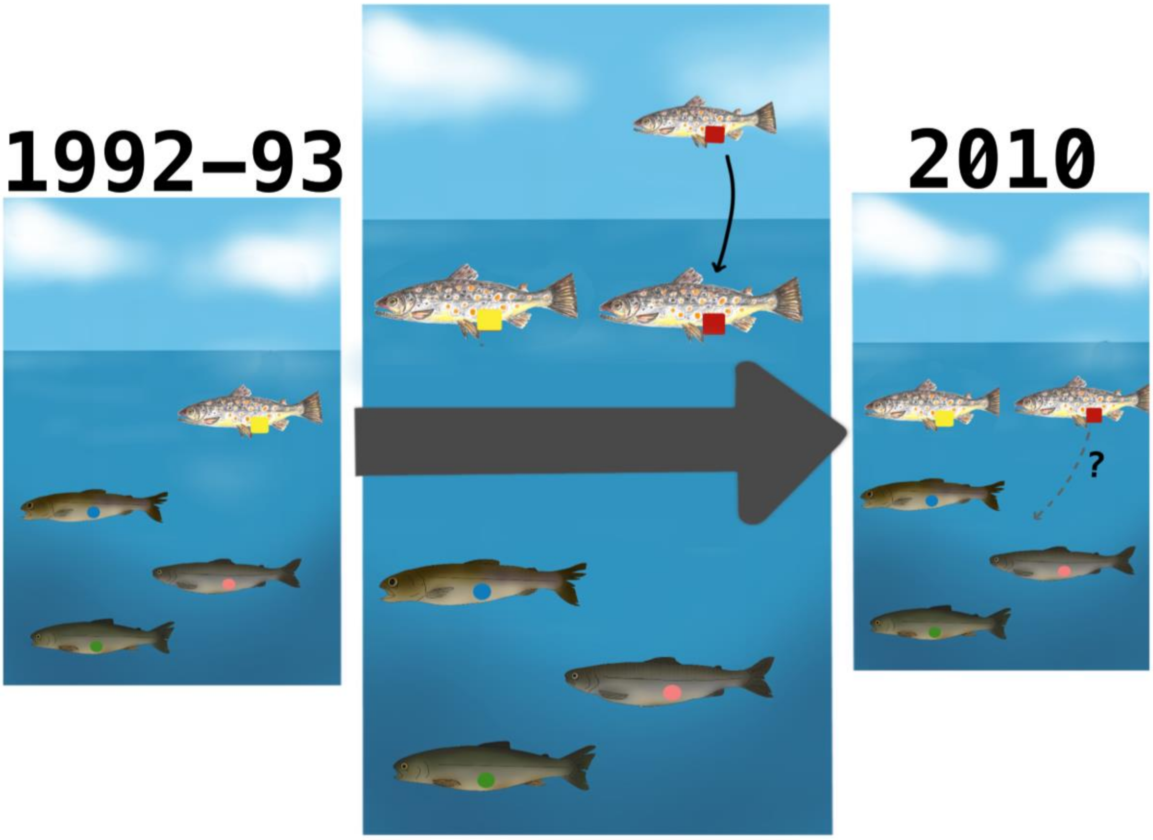

Figure 4: Graphical summary of the results from Paper I show the stability of polymorphic Arctic charr parasite communities over time before and after a fish restock event. Parasite communities are colour-coded according to the fish morph and species (green, benthivore morph; blue, piscivore morph; pink, planktivore morph; yellow, native brown trout; and red, restocked brown trout). The question mark represents the potential influence of the change in the host population (e.g. restock of brown trout) on Arctic charr parasite communities of parasite. Fish drawing made by Nicole Rochat.

2 Summary of results from Paper II

Parasite community re-assembly following eradication: is it predictable?

In this study, the parasite communities in Arctic charr before and after fish host eradication and restocking were compared to assess the parasite community re-establishment after short perturbation events.

In the second study, a total of 17 parasite taxa were identified across three lakes using morphological and genetic analyses, with 12 taxa identified to species and five to genus level. The parasite infracommunity structure differed through time among the lakes and between treated and untreated lakes. Luktvatnet, the control lake, had a stable infracommunity with 12 parasite taxa, including some rare ones.

The treated lakes, Fustvatnet and Ømmervatnet, initially had diverse parasite infracommunities, but after rotenone treatment, a substantial reduction was observed in species composition, abundance, and prevalence. Trematodes became more common post-treatment, while cestode commonness decreased initially before increasing again. The abundance of parasites with complex and simple life cycle showed significant changes post-treatment, with simple life cycles becoming less abundant in the two treated lakes.

The mean parasite infracommunities composition in 2019 were close to, or similar to, their pre-treatment state from 2010-12, and the infracommunities of the treated lakes became more similar in the last two years. The variance of parasite infracommunities was also associated with fish length and showed significant changes over the years, indicating dynamic shifts in parasite communities in response to rotenone treatment and subsequent re-establishment of host communities.

Main conclusions

This study showed an initial decline in parasite communities following the complete eradication of fish hosts in two treated lakes (Figure 5). However, these communities showed resilience, gradually returning to their pre-treatment states after seven years. The shifts in parasite abundance and composition, such as the increase in trematodes and the decline in parasites with simple life cycles, highlight how community dynamics are influenced by drastic ecological changes. The taxon-specific patterns in re-establishment observed, along with the resilience of the parasite community structure and the complexities of species interactions, emphasize the importance of long-term monitoring. Surprisingly, parasite with complex life showed a relative high degree of resilience, regardless of auto- or allogenicity, following short perturbation events.

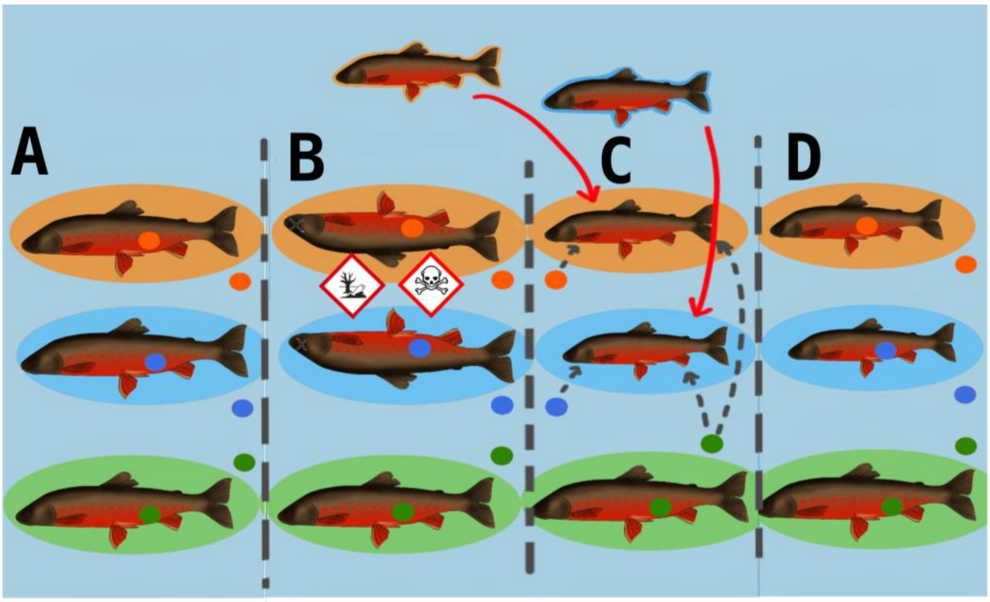

Figure 5: Graphical summary of the results from Paper II showing Arctic charr parasite communities re-establishment after an eradication treatment and fish restock event (two treated lakes: orange – Fustvatnet, blue – Ømmervatnet and one untreated lake: green – Luktvatnet). A: parasite community before the eradication treatment. B: eradication treatment. C: Arctic charr restocking in fall 2013 and spring 2014. D: parasite community after the treatment. The red arrows represent the fish restocking. The dotted grey arrow represents the parasite community re-establishment. The dots correspond to the freshwater parasites infecting Arctic charr (colour coded according to the lake), in Arctic charr (on the fish) or in their intermediate host (beside the fish). Fish drawing made by Nicole Rochat.

3 Summary of results from Paper III

Assessing parasite communities in anadromous Arctic charr: is it a cost of migration?

In this study, the parasite communities in Arctic charr before and after feeding migration were compared to assess the influences of marine migration on parasite community stability and recovery.

The results of the third study showed a total of 22 parasite taxa infecting anadromous Arctic charr. Among these, 19 species were found in migrants, and 16 species were observed in pre- and post-migrants from the lake. Endoparasites constituted the majority (64%) of the observed parasite taxa. Notably, all fish examined harboured at least one parasite species, with *Diplostomum* sp. being the most prevalent across all sampling locations and life history stages.

Pre-migrant charr in the lake were exclusively infected with freshwater parasites. Conversely, migrants from Buktelva exhibited infections from both marine and freshwater parasites. Post-migrant charr in the lake had low prevalence and abundance of marine parasite infestations but were infected with several freshwater parasite taxa.

The analysis of parasite richness revealed no difference between 2020 and 2021 migrants but significant variation among pre-migrants, migrants, and post-migrants. Migrants showed higher parasite taxon richness compared to pre- and post-migrants, with post-migrants having the lowest richness. Contrastingly, parasite abundance varied between 2020 and 2021 migrants, with larger fish exhibiting higher parasite loads, particularly trophically transmitted parasites. Migrants consistently had greater parasite abundance compared to pre- and post-migrants, with trophically transmitted parasites contributing significantly to the disparity. Post-migrants harboured more actively transmitted parasites compared to migrants.

A distinct segregation was observed in the parasite infracommunity structure between migrants and pre/post-migrants sampled in the lake (Figure 6). Differences were also noted between migrants from 2020 and 2021, likely attributed to variations in trophically transmitted parasite abundance. The fish weight and age influenced the parasite infracommunity richness and abundance, contributing to differences in host-parasite dynamics.

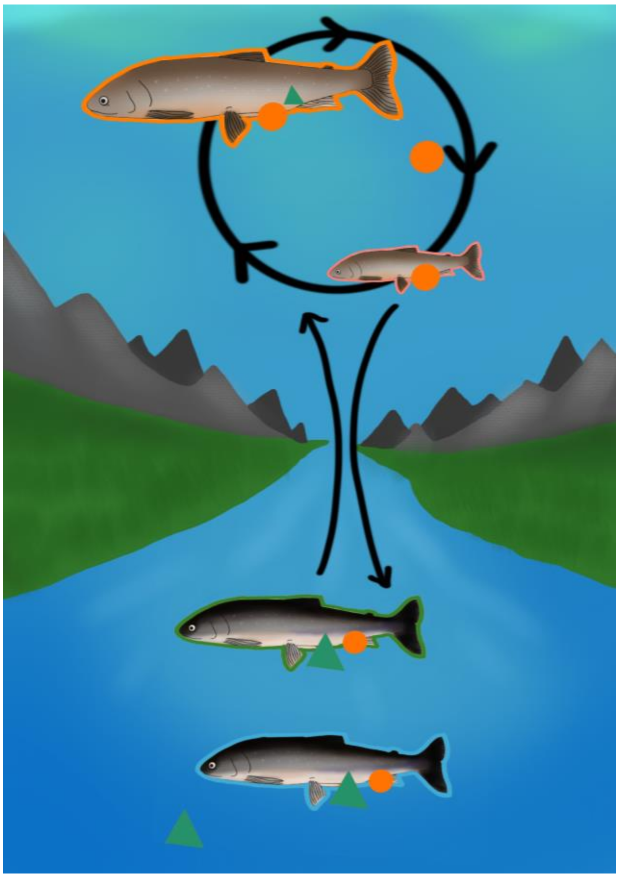

Figure 6: Graphical summary of the results from Paper III showing Arctic charr parasite communities in anadromous Arctic charr. Fish are colour-coded according to the fish group (pink, pre-migrant; green, migrant 2021; blue, migrant 2021; orange, post-migrant). The dots and triangle represent parasite communities and are colour coded according to the parasite origin (orange dots, freshwater and green triangles, marine). The symbol size reflects the abundance of the marine and freshwater parasites. Fish drawing made by Nicole Rochat.

Main conclusions

Paper III highlights that migratory Arctic charr displayed higher parasite taxon richness and abundance compared to their non-migratory counterparts, largely due to increased exposure to diverse parasitic species during marine migration. The distinct parasite infracommunity structures between migratory and non-migratory fish further illustrate the significant role of life history traits in shaping ecological interactions. The variation in parasite abundance influenced by the fish's size and age emphasizes the complexity of these interactions. However, post-migrants harboured only a few marine parasites showing that marine parasites are either eliminated or have a perished. It also remains unclear to what extent parasitism contributes to the high mortality rate in migratory fish in general and anadromy specifically. Thus, although the surviving migrants sustain significant parasite infection burdens during migration, the overall benefits of enhanced growth and reproductive success, combined with mechanisms like migratory recovery, may counterbalance these parasitic costs.

Discussion

The research presented in this thesis significantly advances our understanding of the dynamics governing parasite communities within freshwater ecosystems, particularly in relation to host behaviours and environmental disturbances. This work showed the stability and ability to recover of parasite communities from changes in the host community (e.g. fish restocking, eradication and migration), which extends existing knowledge and provides new insights. The findings from the three studies not only contribute to the academic field but also have practical implications for ecological management and conservation strategies.

Ecological research into parasite communities often focuses on static snapshots of host-parasite interactions without fully considering the temporal and spatial dynamics influenced by host mobility and environmental changes (Lafferty & Kuris, 2002). Many short-term studies might therefore underestimate the resilience of parasite communities to disturbances and their capacity to maintain stability despite significant changes in host populations and environmental conditions (e.g. Lafferty & Kuris, 1999; Alizon & van Baalen, 2008). The findings across the three studies of this thesis contributed to a nuanced understanding of the resilience and adaptability of these parasite communities under various environmental pressures. Throughout the studies presented, we see that despite significant ecological disruptions, ranging from host restocking and species introductions to complete host eradication, parasite communities exhibit a robust capacity to maintain their structure and functionality.

The unique parasite communities within various host morphs in **Paper I** remained stable despite the introduction of new species and restocking efforts, indicating an underlying resilience to external fluctuations and a capacity to adapt to new host dynamics without loss of function or diversity. This stability contrast with previous studies reporting negative influences of environmental disturbance on parasite community composition (e.g. Poteet, 2006; Wood *et al.*, 2023). In **Paper I**, when the host community compositions changed, the parasite communities remained stable, suggesting that the host have maintained their distinct niche over time despite changes in the local community and environmental condition. **Paper II** further supports the stability of parasite communities by demonstrating how parasite communities can recover to their pre-disturbance states after an eradication event. This recovery process showed the ability of these communities to re-establish an equilibrium over time, in line with ecological resilience theories such as global equilibrium concept (i.e. time required for a system to return to an equilibrium or steady-state following a perturbation, Gunderson (2000)). **Paper III** extended on this discussion by showing that migration, a natural host behaviour, enriches and diversifies the parasite communities in each environment instead of making them unstable. This contributes to increase the overall ecological stability of parasite communities by introducing new components into their parasite community structure.

Collectively, these findings contrast with the prevailing notion that parasite communities are susceptible to immediate disruption by changes in host dynamics (e.g. Grenfell & Dobson, 1995; Dobson & Foufopoulos, 2001). It implies a degree of ecological resilience and robustness that allows these communities to act as a buffer against sudden changes, thereby preserving ecosystem unity'. Indeed, the resilience of communities implies a certain degree of stability of parasite community structure, as parasite contribute to the bonding of the network connectivity (Seilacher *et al.*, 2007). In particular **Paper II** provided a compelling illustration of how parasite communities not only withstand initial shocks but also exhibit substantial capacity to reassemble and regain their former diversity and structure in a short time, even after catastrophic events. The underlying processes are likely similar to the effects of environment restauration on parasite communities where parasite community thrive post-restauration (e.g. Lotze *et al.*, 2011; Moore *et al.*, 2020), and return to a steady-state and ecological equilibrium (Gunderson, 2000). This recovery is not instantaneous but progresses through a series of ecological successions, where different species recolonize and reestablish their populations over time (e.g. Rasheed, 2004; Lotze *et al.*, 2011). This goes with ecological theories on secondary succession and resilience (e.g. Shabarova *et al.*, 2021), suggesting that these communities possess inherent recovery pathways that are triggered by disturbances (e.g. Connell & Slatyer, 1977; Poulin, 2014).

Parasite community stability and recovery observed could be associated with adaptability. Parasites with complex life cycles include multiple stages, some of which may involve different hosts or environmental conditions (Rózsa & Garay, 2023). These complex life cycles can show some plasticity, allowing parasites to withstand changes in the environment or host availability by stopping their development or switching routes in their transmission cycle (e.g. Gervasi *et al.*, 2015; Aleuy & Kutz, 2020). Moreover, parasite communities can undergo ecological succession, a process where community structure and species composition gradually change over time or seasonally (e.g. Kuhn *et al.*, 2016; Prati *et al.*, 2020). This succession mechanism can participate in the recovery of parasite communities after change in host behaviours or environmental disturbances, by allowing different species to thrive at various stages, eventually leading to a restored equilibrium (e.g. in freshwater microbial communities: Shabarova *et al.*, 2021).

Furthermore, an important factor driving the parasite community stabilities could be the environmental and host stability itself (e.g. Anderson & Sukhdeo, 2013). Indeed, the ecosystem is important for parasite communities' recovery, assembly and stability (e.g. Anderson & Sukhdeo, 2016; Gouezo *et al.*, 2019), just like parasites have a significant impact on the stability of ecosystems (e.g. McQuaid & Britton, 2015; Mougi, 2022). At a metacommunity level, communities of parasites can occupy various hosts and are connected by dispersal of multiple, potentially interacting species (Leibold *et al.*, 2004). This spatial structuring can help the recolonization of disturbed areas, ensuring long-term parasite community stability. My findings increase our understanding of how parasite communities stay stable in a single host population or across systems, when influenced by ecological changes in their host population. They showed how changes in one part of a wider metacommunity, such as the introduction or removal of species within a host community (**Paper I** and **II**) or the migration patterns of hosts (**Paper III**), can have impacts through the entire network, affecting parasite diversity and distribution on a larger scale.

Paper III's examinations further our understanding of parasite communities in migrants by showing that migration can be resilience by flipping between two stable freshwater and marine parasite communities. While the impact of migration on host fitness and population dynamics has been well-documented (see Alerstam *et al.*, 2003; Dingle, 2014; Shaw, 2016), its specific effects on parasite community structure and transmission dynamics have been less explored (Poulin & De Angeli Dutra, 2021). My study demonstrates that migratory hosts harbour more diverse and abundant parasite communities than their non-migratory counterparts, likely due to exposure to a broader range of environments and potential parasite sources. Indeed, the host migration facilitates new interactions and transmission opportunities for parasites (Altizer *et al.*, 2011). This shows that migration is an ecological force that increases the complexity of parasite communities and strengthens their resilience and stability in multiple environments.

Moreover, migration can act as a mechanism for spreading parasites and a strategy for escaping them, depending on the circumstances (e.g. Shaw & Binning, 2016; Peacock *et al.*, 2020; Poulin & De Angeli Dutra, 2021). Therefore, migration can contribute to make a more robust systems capable of faster recovery from disturbances and help the overall resilience of ecosystems (Lymbery & Smit, 2023). My study results suggested that migratory behaviours significantly contributes to the interconnection of parasite communities and the environment (Bauer & Hoye, 2014). This interconnectivity is crucial for maintaining ecological balance and function within and across ecosystems, underscoring the importance of considering metacommunity dynamics in ecological and conservation strategies (e.g. Holyoak *et al.*, 2005; Thompson & Gonzalez, 2017). Exploring the dynamics of parasites communities in dynamic host environment offers key highlights into the interplay between host movement, surrounding and parasite diversity in dynamic environments.

The understanding of how environmental changes affect host-parasite dynamics can greatly inform conservation strategies (e.g. Hudson *et al.*, 2006; Carlson *et al.*, 2020). It's imperative to consider the broader implications of these findings in a rapidly changing world (e.g. Lafferty & Kuris, 1999; Altizer *et al.*, 2011). The findings of my thesis show that parasite communities are surprisingly stable and resilient, and improve our ability to predict and manage ecological recovery in the face of environmental changes (e.g. Lafferty & Kuris, 1999; Marcogliese, 2004; Kéfi *et al.*, 2012). For instance, **Paper I** and **II** can help predict and mitigate the impacts of anthropogenic intervention on parasite communities. Then, **Paper III**'s observations about migratory behaviours increase parasite diversity and help ecosystem resilience suggest that conservation practices should protect critical habitats across both freshwater and marine environments. The environmental changes driven by global climate change, habitat destruction, and increased human activity represent numerous challenges to ecological balance (e.g. Vitousek *et al.*, 1997; Fahrig, 2003; Parmesan & Yohe, 2003).

Parasites are important components of ecosystems and indicators of environmental health (e.g. Palm *et al.*, 2011; Shah *et al.*, 2013) and can play a crucial role in biodiversity assessments and ecosystem management strategies (Marcogliese, 2005; Marcogliese, 2023). The integration of dynamic interactions between parasites and their hosts in ecological models can more accurately predict how ecosystems respond to various disturbances (e.g. Dobson & Foufopoulos, 2001; Gómez & Nichols, 2013), leading to more effective management and policy decisions (e.g. Timi & Poulin, 2020; Lymbery & Smit, 2023). Additionally, the metacommunity perspective highlights the need for conservation approaches that transcend local ecosystems and consider broader geographical scales, acknowledging the interconnectedness of different ecological zones (e.g. Leibold *et al.*, 2022). This holistic view, i.e. understanding the whole system, can guide more effective management of wildlife corridors and buffer zones, which support natural dispersal processes that sustain dynamic and healthy parasite communities and contribute to a more complete understanding of biodiversity and ecosystem function (e.g. Thomas *et al.*, 1999; Marcogliese, 2005; Rubio-Godoy & de León, 2023).

Future prospects

The knowledge generated by my study raises questions about the underlying mechanisms contributing to the observed resilience and stability of parasite communities. While our studies have confirmed that parasite communities can maintain stability over time, the specific factors driving this phenomenon remain somewhat unclear. Future research should focus on elucidating the complex ecological and biological processes that are behind this stability. Moreover, the role of parasites as ecosystem engineers needs greater acknowledgment and understanding (e.g. Jones *et al.*, 1994; Thomas *et al.*, 1999). Therefore, by investigating how parasites influence ecosystem processes and contribute to ecological resilience, we can increase our knowledge on their roles in participating to biodiversity and ecosystem dynamics, as suggested by previous studies (e.g. Knowles *et al.*, 2013; Moore *et al.*, 2020; Schwelm *et al.*, 2021). Such research would benefit from an integrative approach that examines the intricate interactions among multiple species across various ecological niches, including both hosts and their parasites. This prospect could lead to significant advancements in our understanding of ecosystem function and resilience, offering valuable highlight into the broader ecological implications of parasite community stability.

Exploring the full parasite community within ecosystems, including the roles of intermediate hosts, ecosystem recover and stability after disturbances is interesting for future research (e.g. Lafferty *et al.*, 2008; Timi & Poulin, 2020). Such holistic approaches could better highlight the complex life cycles of parasites and the pivotal roles that various hosts play in maintaining or disrupting parasite community. By increasing the scale of studies to encompass intermediate hosts, researchers can better understand the multifaceted interactions that underpin parasite community stability and ecological balance (e.g. Hassell *et al.*, 2021). Such approaches would help unravelling the mechanisms through which parasites influence ecosystem health and improve our ability to predict the impacts of parasitic diseases across multiple trophic levels (e.g. Keyes *et al.*, 2021). This broader perspective could help predicting how changes in habitat induced by anthropogenic activity will impact parasite-host relationships rather than focusing on top predators or final hosts alone.

Conclusion

Overall, the research presented in my thesis offers new insights into the dynamics of parasite communities at a parasite species level. Parasites communities are complex, resilient and have a critical role in ecological processes. My results illustrate how parasite communities are influenced by changes in host populations and environmental disturbances. These parasite communities also seem to play an important role in the stability and recovery of ecosystems. These parasites are not isolated; they are integrated into ecological networks, moving through trophic levels and influencing energy flows and nutrient cycles. These results go against most of the traditional views of parasitism as a negative interaction, and instead position them as integral components of ecosystems, essential for maintaining biodiversity and ecological balance.

The findings have increased our knowledge of the complex interaction between parasite communities and their hosts within dynamic environments. Through an examination of the impacts of ecological changes, such as restocking, species introductions, eradication, and natural host migrations, these studies have provided novel support for the resilience and stability of parasite communities. These parasite communities have been shown to maintain their structure and functionality despite significant disturbances, continuing to have substantial ecological influence on their hosts. This research suggests that these parasite communities possess mechanisms that allow them to survive and resist environmental changes.

Furthermore, the role of parasites in ecosystems could become even more important for ecosystem stability as we face global environmental changes (e.g. Hassell *et al.*, 2021; Lymbery & Smit, 2023). For instance, the presence and dynamics of parasite communities can provide early warnings of ecological shifts and degradation (e.g. Lanfranchi *et al.*, 2024). Thus, including these often-overlooked parasites in ecological research and management plans can help our understanding of ecological processes and improves our ability to predict, respond to, and manage ecological changes (e.g. Timi & Poulin, 2020; Keyes *et al.*, 2021). Ultimately, the three studies of this thesis contribute to the field of parasite ecology, particularly in regions experiencing rapid environmental change and biodiversity loss such as Northern region. This thesis supports a comprehensive approach to ecological research, by highlighting the complexity and interconnection of all free-living and parasitic organisms within ecological networks.

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Papers

Paper I

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RESEARCH ARTICLE

Temporal stability of polymorphic Arctic charr parasite communities reflects sustained divergent trophic niches

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Abstract

Polymorphic Arctic charr *Salvelinus alpinus* populations frequently display distinct differences in habitat use, diet, and parasite communities. Changes to the relative species densities and composition of the wider fish community have the potential to alter the habitat niche of sympatric Arctic charr populations. This study evaluated the temporal stability of the parasite community, diet, and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) of three sympatric Arctic charr morphs (piscivore, benthivore, and planktivore) from Loch Rannoch, Scotland, in relation to changes to the fish community. All Arctic charr morphs displayed distinct differences in parasite communities, diet, and stable isotope signatures over time, despite the establishment of four new trophically transmitted parasite taxa, and increased fish and zooplankton consumption by the piscivorous and planktivore morphs, respectively. Native parasite prevalence also increased in all Arctic charr morphs. Overall, Loch Rannoch polymorphic Arctic charr morph populations have maintained their distinct trophic niches and parasite communities through time despite changes in the fish community. This result indicates that re-stocking a native fish species has the potential to induce shifts in the parasite community and diet of Arctic charr morphs.

KEYWORDS
introduced species, *Salvelinus alpinus*, Scotland, stable isotopes, trophically transmitted parasites

TAXONOMY CLASSIFICATION
Parasitology

1 | INTRODUCTION

Freshwater systems are the most threatened ecosystems on earth (Albert et al., 2021; Kernan et al., 2011; Reid et al., 2019; Woodward et al., 2010). Furthermore, human-induced global change has placed severe pressure on aquatic ecosystem structure and function, and poses a considerable threat to biodiversity (e.g., Christensen et al., 2006; Ficke et al., 2007; Jackson et al., 2016) and food webs (Nagelkerken et al., 2020; Petchey et al., 1999). Model predictions suggest the geographic distributions of many fish species, including Arctic charr (*Salvelinus alpinus* L.), will be significantly reduced as a result of climate warming (Chu et al., 2005; Hein et al., 2012; Svenning et al., 2022). Moreover, given the importance of biological interactions as drivers of ecological processes (Blois et al., 2013), freshwater fish communities have the potential to be highly affected by several other commonly conducted anthropogenic activities. For

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instance, fish re-stocking and fish introduction can impact the native fish community (Britton et al., 2011) by modifying inter- and intraspecific competition for food, habitat, and niche space between fish species (e.g., Britton et al., 2010; Gregersen et al., 2006; Klemetsen et al., 2003), parasite component communities (i.e., parasites found in a host population, here in a morph; e.g., "spillback" impact on native fishes; Kelly et al., 2009) and changes in predator–prey relationships (L'Abée-Lund et al., 1992). Arctic charr is the world's northernmost freshwater fish species (Klemetsen et al., 2003) and thus represents an interesting model species to study the influences in multiple anthropogenetic stressors occurring at the southern edge of this species' geographic distribution.

Arctic charr express high levels of phenotypic plasticity, with up to five different morphs known to co-occur in a single water body (Doenz et al., 2019; Skúlason et al., 1989), and may also form genetically segregated populations (Moccetti et al., 2019; Præbel et al., 2016; Simonsen et al., 2017; Verspoor et al., 2010). Sympatric Arctic charr morphs can be distinguished by their size, head morphology, and stable isotope tracers (δ^{15}N and δ^{13}C), the stable isotope value of which depends on foraging habits (Doenz et al., 2019) and trophic niche (e.g., Adams et al., 2003). Commonly, morphs segregate along the benthic-pelagic resource axes where one morph feeds in the benthic environment (benthivore morph) and one morph relies more heavily on food available in the water column (planktivore morph; Adams, 1998; Skúlason et al., 1989; Walker et al., 1988). A piscivore Arctic charr morph may occur in either the upper water (Adams, 1998; Sandlund et al., 1992) or deep in the profundal zone (e.g., Knudsen, Amundsen, et al., 2016; Knudsen, Gjelland, et al., 2016; Power et al., 2005).

Arctic charr are known to host more than 40 metazoan parasites (Moravec, 2004). The diversity of their parasite community is attributed to their diet since most known parasite taxa of Arctic charr are trophically transmitted via the consumption of intermediate hosts, often invertebrates or small fish (Moravec, 2004). Thus, Arctic charr morphs are exposed to different parasite communities depending on habitat choice, feeding habits, and the presence of the intermediate hosts in their occupied habitat (Frandsen et al., 1989; Jonsson & Jonsson, 2001; Knudsen et al., 1997; Sandlund et al., 1992). In this context, trophically transmitted parasite communities can reveal the temporal stability of the food web (Behnke et al., 2018), since their complex life cycles span multiple trophic levels.

In this study, we evaluated the temporal stability of the parasite infracommunity of a polymorphic Arctic charr population in Loch Rannoch following brown trout *Salmo trutta* (L.) re-stocking and crucian carp *Carassius carassius* (L.) introduction (see Fraser & Adams, 1997). A risk exists that introduced fish species bring alien generalist parasites that successfully establish in native fish (e.g., Asian fish tapeworms and yellow grub; Dove et al., 1997; Gaglio et al., 2016; Kuchta et al., 2018), although most parasites tend to be specialized in one or few types of host. While brown trout were already part of the native community, trout originating from a different lake/hatchery are potentially exposed to different parasites, and thus may introduce novel parasite taxa to the system (i.e., a translocation impact: Kelly et al., 2009; Peeler et al., 2011). Arctic charr and brown trout share many parasite species that can be translocated along with the host and establish in the local fish community (e.g., Adolfsen et al., 2021; Bristow, 1993; Knudsen et al., 2007). The parasite load in the system can be indirectly amplified (Kelly et al., 2009) or diluted (Goedknegt et al., 2016) as higher salmonid density can act as an enlarged pool of hosts for native parasites. In addition, the brown trout and crucian carp are two benthivore fish and they could compete for common resources with Arctic charr (Eloranta et al., 2013; Langeland et al., 1991). It is also possible that introduced fishes cause indirect changes in the parasite community of Artic charr through modifying predator–prey links that expose hosts to a different range of parasites or by acting as parasite sinks themselves, thus reducing Arctic charr exposure (Poulin & Mouillot, 2003).

Overall, the Arctic charr parasite community in Loch Rannoch might change through time due to the introduced-relocated benthivore competitor (e.g., brown trout and crucian carp) or other possible explanations (i.e., annual variability). This increase in benthivore fishes might promote the copepods transmitted parasite (Dorucu, 1996; Dorucu, Adams, et al., 1995). However, the parasite community of the three morphs of Arctic charr might still be different if their diet and habitat are stably diverged through time (Dorucu, 1996). Indeed, we expect that Arctic charr morphs maintain trophic niche partitioning. Thus, we hypothesized that: (a) trophic niches of the three Arctic charr morphs will be stable through time (i.e., diet and isotope); thereby (b) the parasite component communities in Arctic charr morphs will remain distinctly different between morphs as all the taxa previously recorded are trophically transmitted. These two hypotheses are assessed in this study using a contemporary snapshot of the trophic information provided by diet analysis and the proxies of longer-term trophic niche provided by stable isotope analyses (δ^{13}C, δ^{15}N) and parasite communities.

2 | MATERIAL AND METHODS

2.1 | Study area and samples collection

Loch Rannoch is an oligotrophic lake in the Tayside Region, Scottish Highlands (56°41′N; 004°17′W, 17 km^2, 203 m above sea level, 134 m maximum depth; Bryce et al., 2016). Loch Rannoch's fish community is composed of eight native fish species (Arctic charr, brown trout that is often re-stocked, pike *Esox lucius* L., perch *Perca fluviatillis* L., minnow *Phoxinus phoxinus* L., three-spined stickleback *Gasterosteus aculeatus* L., European eel *Anguilla anguilla* L., Atlantic salmon *Salmo salar* L.; Verspoor et al., 2010; Walker et al., 1988) and an alien species recorded for the first time in 1997, the crucian carp (Fraser & Adams, 1997). Moreover, the Arctic charr population in Loch Rannoch comprises three morphs (a littoral benthivore, planktivore, and profundal piscivore morph; Adams et al. (1998)), which differ in terms of their functional trophic morphologies (Adams & Huntingford, 2002; Bryce et al., 2016), life-history traits (Adams & Huntingford, 2004; Fraser et al., 2008), trophic niches (Adams et al., 1998) and parasites (Dorucu, 1996). However, the relative amount of each species is unknown.

Arctic charr were sampled using gill nets in October 1992 and July 1993 (*n* = 253; see Dorucu, Adams, et al. (1995), Dorucu (1996) for details), and in October 2010 (this study, *n* = 101). Gill nets were deployed overnight for a maximum period of 12 h during both study periods. Between 1992 and 93, 30 benthivore, 173 planktivore, and 50 piscivore Arctic charr were collected. In 2010, 34 benthivore, 34 planktivore and 33 piscivore Arctic charr were sampled (Table 1). All fish were frozen and transported to the Scottish Centre for Ecology and the Natural Environment (SCENE), University of Glasgow for subsequent analysis (Adams et al., 1998). Fork length (mm) was measured for all sampled fish.

2.2 | Diet analyses

The stomach fullness was determined from the dissection of the alimentary canal. Stomach contents collected from the upper end of the esophagus to the pyloric sphincter were identified to the lowest practical taxonomic level (typically order or family) under a stereomicroscope. The diet groups identified in 1992–93 (Dorucu, 1996) served as a reference point for the analyses in 2010 (zooplankton, copepods, surface insects, chironomid larvae, *Pisidium*, insect larvae, *Gammarus*, unidentified invertebrates, fish). The frequency of occurrence of each prey category was evaluated as volume percentage for each stomach and each food category (Hyslop, 1980). Schoener's index (Wallace Jr, 1981) was used as a proxy for diet overlap between different morphs in each time period and the two sampling periods for each morph. This index is usually considered as biologically meaningful when its value exceeds 60% (Wallace Jr, 1981). For comparison, the frequency of occurrences of each prey in 1992–93 was extracted from Dorucu (1996) using DataThief III software (Tummers, 2006).

2.3 | Parasitological analyses

Parasite prevalence (i.e., proportion of host individuals of an Arctic charr morph that were infected) and mean abundance (i.e., the mean number of parasites in a given host morph) were calculated for each parasite species (Bush et al., 1997). In our study, the parasite prevalence data for Arctic charr from 1992–93 were obtained from Dorucu (1996) using DataThief III software (Tummers, 2006). The fish sampled in 2010 were examined for metazoan parasites using a stereomicroscope, with parasites morphologically identified to species or genera using taxonomical criteria (e.g., Moravec, 2004) before specimens were fixed in absolute ethanol for molecular analyses. We selected some of the specimens used for the morphological analyses and rehydrated them, as preservation in absolute ethanol shrink and/or modify the internal structures of the worms. We prepared whole mounts according to Cribb and Bray (2010) and Justine et al. (2012) protocols. Unfortunately, the preservation quality of the specimens (e.g., poor quality tubes and wrong concentration of alcohol) did not allow a more accurate morphological identification, and molecular identification was needed.

TABLE 1 Arctic charr sampled in Loch Rannoch (1992–93 from Dorucu, Adams, et al. (1995) and 2010).

Years	1992–93		2010	
Morph	*N*	Size (min.–max.) mm	*N*	Size (min.–max.) mm
Benthivore	30	194.0 (148–235)	34	206.3 (130–309)
Planktivore	173	186.4 (80–225)	34	234.1 (192–263)
Piscivore	50	191.6 (60–265)	33	288.2 (164–373)

Molecular data were obtained from a subsample of specimens for each prospective parasite taxa (from 2010 only) to confirm their morphological identification. DNA was extracted using Chelex® in deionized water containing 0.1 mg/ml proteinase K. A partial fragment of the large ribosomal subunit (28S rDNA) was chosen as a marker because it is broadly used to molecularly assign parasitic flatworms and acanthocephalans to known genera/species (Blasco-Costa et al., 2016) and a partial fragment of the small ribosomal subunit (18 S rDNA) was amplified for the nematodes since it is the most common marker used for this group (Černotíková et al., 2011). The following primers were used for the amplification of acanthocephalans, U178 (forward; 5′-GCA CCC GCT GAA YTT AAG-3′) and L1642R (reverse; 5′-CCA GCG CCA TCC ATT TTC A-3′; Lockyer et al., 2003); and of the nematodes, PhilonemaF (forward; 5′-GCC TAT AAT GGT GAA ACC GCG AAC-3′) and PhilPCRr0 (reverse; 5′-CCG TT CAA GCC ACT GC ATT A-3′; Černotíková et al., 2011). In addition, the cytochrome c oxidase subunit I mitochondrial gene (COI) was also amplified using Plat-diploCOX1F (forward; 5′-CGT TTR AAT TAT ACG GAT CC-3′) and Plat-diploCOX1R (reverse; 5′-AGC ATA GTA ATM GCA GCA GC-3′; Moszczynska et al., 2009). The PCR amplification protocol for the 28 S marker followed Blasco-Costa et al. (2009), for the 18 S followed Černotíková et al. (2011) and for the COI followed Blasco-Costa et al. (2014). Purified amplicons were sent to Macrogen Europe (Amsterdam, Netherlands) for sequencing from both strands, with the same PCR primers used for amplification.

Sequences were assembled and inspected for errors using Geneious® ver. 8.1.9 (Kearse et al., 2012) and submitted to GenBank® (accession numbers in Table S1). Available sequences for taxa belonging to the same family/genus/species as our presumed taxa were obtained from GenBank® and aligned with our sequences to validate species identification or improve the preliminary identification based on specimen morphology. Following this, alignments were obtained using the default parameters in MAFFT (Katoh et al., 2005) and were trimmed at their extremities.

Parasite phylogenetic reconstructions were carried out using maximum likelihood (ML) and Bayesian inference (BI) criteria. The model of nucleotide evolution GTR (general time-reversible model) with a gamma distribution using among-site rate variation (Γ) was applied to all analyses. ML analyses were conducted using RAxML ver. 8 (Stamatakis, 2006). All model parameters and bootstrap nodal support values (1000 repetitions) were estimated in RAxML. BI trees were constructed using MrBayes ver. 3.2.6 (Ronquist et al., 2012), running two independent MCMC runs of four chains for 10 million generations and sampling tree topologies every 1000th generation. Burn-in periods were automatically set to 25,000 generations. RAxML and MrBayes analyses were carried out for each individual dataset on the public computational resource CIPRES (Miller et al., 2011).

2.4 | Stable isotope analyses

Dorsal muscle tissue samples from 32 benthivore, 32 planktivore, and 21 piscivore Arctic charr sampled in 2010 were dried at 50°C for 24h, before being ground to a fine powder with a mortar and pestle, and weighed for analysis (0.3 mg). Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes were then analyzed from individual fish at the University of Waterloo, Canada, using a dual inlet Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) connected to a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA). Obtained stable isotope ratios were expressed in standard delta notation (‰) relative to the international reference materials of Vienna PeeDee Belemnite for carbon (Craig, 1957) and atmospheric nitrogen (Mariotti, 1983). Data quality control was monitored, and corrections were made using a mix of international and in-house standards (e.g., cellulose and bovine liver) cross-calibrated against International Atomic Energy Agency standards for Carbon (CH3, CH6) and nitrogen (N1, N2). No <20% of the samples included in any run consisted of standards and reference materials, with obtained measurements used in data normalization and to ensure measurement precision and accuracy. Associated QC/QA checks indicated an error for reportable data of no more than 0.2‰ and 0.3‰, respectively, for δ^{13}C and δ^{15}N.

2.5 | Statistical analyses

All the analyses were computed with the statistical software R version 4.1.0 (www.r-project.org). Separate generalized linear models (GLM) were used to investigate the influence of fish morph (benthivore, planktivore, piscivore) and fish length on species richness, total parasite taxa abundance, and the abundance of each parasite taxon among the three Arctic charr morphs (2010 only). Models were fitted with appropriate Poisson or quasi-Poisson distributions, to account for over-dispersion (see Tables S2 and S3) detected by *AER::dispersiontest* (Kleiber & Zeileis, 2008). Additionally, the correlation of variables was assessed using the function *corPlot::psych* (Revelle, 2011) and *cor.test::stat* (R Core Team, 2021), and interactions between variables were included in the GLM models when taxa were correlated with another variable (i.e., fish length in our model).

Dissimilarity among the parasite infracommunities (i.e., parasite taxa abundance of an individual fish) in 2010 as a function of Arctic charr morph (Krebs, 1999) was assessed with nonmetric multidimensional scaling (NMDS) analyses using the zero-adjusted, Bray–Curtis dissimilarity measure, which is not affected by the number of null values between samples (Clarke et al., 2006). To account for species absences in some infracommunities (zero-inflated data) a "dummy species" was added to all communities (see Clarke et al. (2006)). The significance of the predictor variables (i.e., fish morph), was tested with the Adonis function. These analyses were conducted with the package *vegan* (Oksanen, 2020) and *MASS* (Venables & Ripley, 2002).

Multivariate analysis of variance tests (MANOVA) and Wilcoxon tests were used to decide whether the distributions of δ^{13}C (reflecting the origin of the carbon in the tissue of the fish) and δ^{15}N (reflecting its trophic position) values among the three Arctic charr morphs differed (2010 only). The isotopic niche overlaps were also assessed between Arctic charr morphs using a Bayesian approach derived from Swanson et al. (2015) implemented in the package *nicheROVER* (Lysy et al., 2014). This method provides the 95% probability and credibility interval that one individual from one morph could be found within the niche of another morph.

3 | RESULTS

3.1 | Stomach contents

In 2010, 39.3% of the planktivore morph Arctic charr had empty stomachs, with the remaining individuals having low stomach fullness (mean ± SE; 17.7 ± 5.2%; Figure 1a). This contrasts with the benthivore morph with only 5.7% of individuals having empty stomachs and a stomach fullness of 54.2 ± 5.5%. By contrast, the piscivore morph showed intermediate values of empty stomachs (22.2%) and stomach fullness (31.1 ± 6.4%). Diet differed among the three morphs. Piscivores had a low diet overlap with both the benthivore morph (18.8%) and the planktivore morph (27.8%) due to a high consumption of fish (69.1%). Diet overlap between the benthivore and planktivore morphs (70%) was high as both morphs preyed heavily on chironomid larvae (55.9 ± 5.3% and 52.3 ± 10.7%, respectively). Zooplankton (*Daphnia* and *Polyphemus*) were mainly found in the diet of the planktivore morph (29.7 ± 11.5%). The benthivore morph consumed more *Pisidium* clams (13.6 ± 2.6%), *Gammarus* (0.7 ± 0.3%), and large insect larvae (10.2 ± 5.1%) than the planktivore morph. The largest dietary changes between 1992–93 and 2010 included increased consumption of fish (+59.57%) and decreased chironomid larvae (−47.2%) by the piscivore morph, and reduced consumption of copepods (−47.0%) and increased chironomid larvae (+36.3%) by the planktivore morph (Figure 1a). All other differences between the two sampling periods were minor (<24%).

3.2 | Parasite communities

Eleven parasite taxa, of which three allogenic taxa that mature in fish and seven autogenic taxa that mature in terrestrial vertebrates

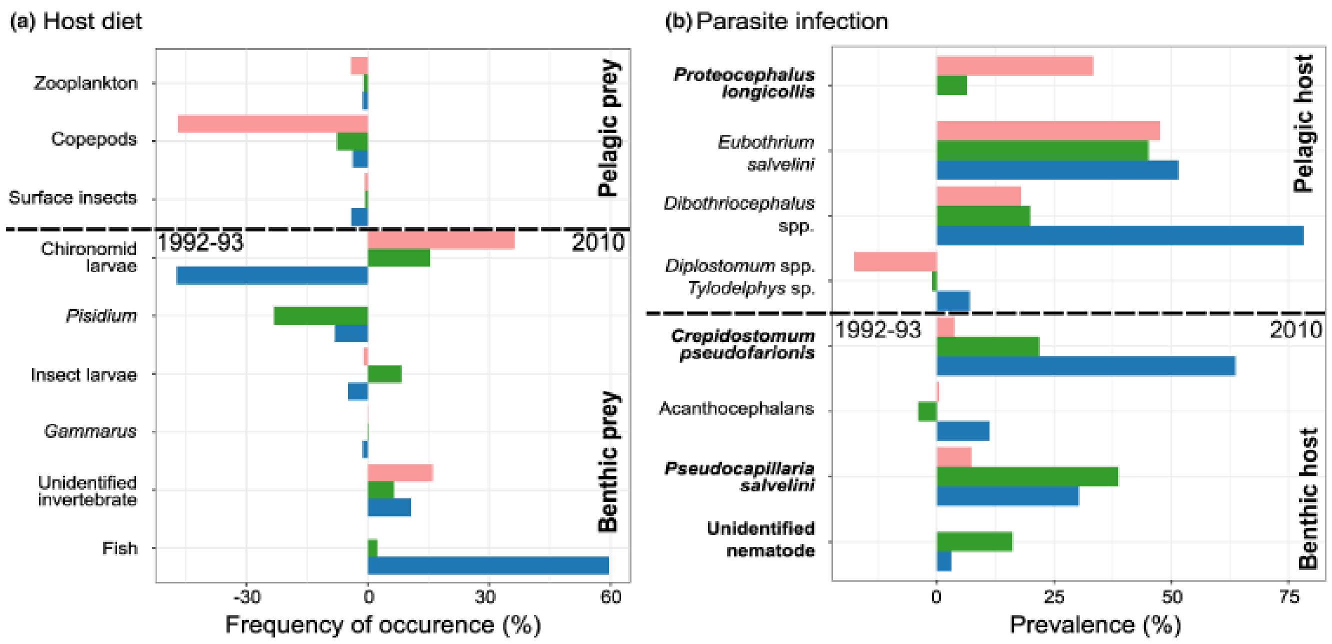

FIGURE 1 Comparisons between the periods of 1992–93 (at the left) and 2010 (at the right) and among the Arctic charr morphs. (a) Frequency of occurrence of prey items. (b) Parasite infection prevalence. Note that values for the acanthocephalans (*E. truttae* and *N. rutili*), *Dibothriocephalus* (*D. dendriticus* and *D. ditremus*), and eye flukes (*D. baeri*, *Diplostomum* sp. and *Tylodelphys* sp.) are grouped. Bar colors refer to fish morph: green—benthivore morph; blue—piscivore morph; and pink—planktivore morph.

(Esch et al., 1988), were identified from Arctic charr sampled in 2010 (Figure 1 and Table 2). The seven species recorded in 1992–93 included the acanthocephalans *Echinorhynchus truttae* (Schrank, 1788) and *Neoechinorhynchus rutili* (Müller, 1780), the trematodes *Diplostomum* spp., and *Tylodelphys* sp.; the cestodes *Dibothriocephalus* spp. (*D. dendriticus* and *D. ditremus*; formerly *Diphyllobothrium* spp. synonymized in Waeschenbach et al. (2017)) and *Eubothrium salvelini* (Schrank, 1790; Dorucu, 1996; Dorucu, Crompton, et al., 1995). In addition to the species above, four taxa were recorded for the first time in 2010, the trematode *Crepidostomum* sp., the cestode *Proteocephalus longicollis* (Zeder, 1800), and two nematodes, *Pseudocapillaria (Ichthyocapillaria) salvelini* (Polyansky, 1952) and one other species unidentifiable based on morphology due to the preservation quality.

Molecular data and phylogenetic analyses corroborated the morphological identification of the new trematode as *Crepidostomum* and further confirmed the identification of the species as *Crepidostomum pseudofarionis* Faltýnková, Pantoja, Skírnisson and Kudlai, 2020 (Figure 2a and GeneBank number: OP580487). The morphological identification of *E. truttae* was also confirmed by molecular methods (Figure 2b and GeneBank number: OP580482 to OP580486). Additionally, three different lineages of *Diplostomum* were molecularly characterized, two of *Diplostomum baeri* Dubois, 1937 and one unidentified *Diplostomum* sp. (Figure 2c and GeneBank number: OP577853 to OP577862). The preservation quality of the specimens of an unknown nematode and *Tylodelphys* sp. did not permit identification to the species level.

3.3 | Parasite component communities among Arctic charr morphs

In addition to the presence of four previously undetected parasite taxa in Arctic charr, the prevalence of parasites increased in each morph between 1992–93 and 2010 (see Figure 1b and Table 2).

The total prevalence of parasite infection was high in the fish sampled in 2010, 100% of the piscivore and planktivore morphs and 88.2% of the benthivore morph. The piscivore morph showed a significantly higher overall parasite abundance than the benthivore morph, which also showed a higher overall parasite abundance than the planktivore morph (Table 2). The three morphs showed distinctive patterns of infection with differences in parasite prevalence (Figure 1b and Table 2). The eye flukes (*Diplostomum* spp. and *Tylodelphys* sp.) and the two nematode taxa (*P. salvelini* and the unknown nematode) were more common in benthivore morph (see Table 2). The cestode taxa, *Dibothriocephalus* spp. and *E. salvelini* were more common in the planktivores (94 and 68%, respectively) than in the piscivores (88 and 51%) or benthivores (21 and 45%, respectively). *Proteocephalus longicollis* was more common in the planktivores (36%) than in the other morphs. The three remaining taxa (*C. pseudofarionis*, *E. truttae*, and *N. rutili*) were mainly recovered from piscivorous Arctic charr (63% versus <23% in two other morphs for *C. pseudofarionis* and 21% versus <4% in the planktivores for the acanthocephalans). Finally, the two acanthocephalans and the unknown nematode were relatively uncommon (prevalence 0%–21%) in all morphs. Moreover, our results also showed that the overall

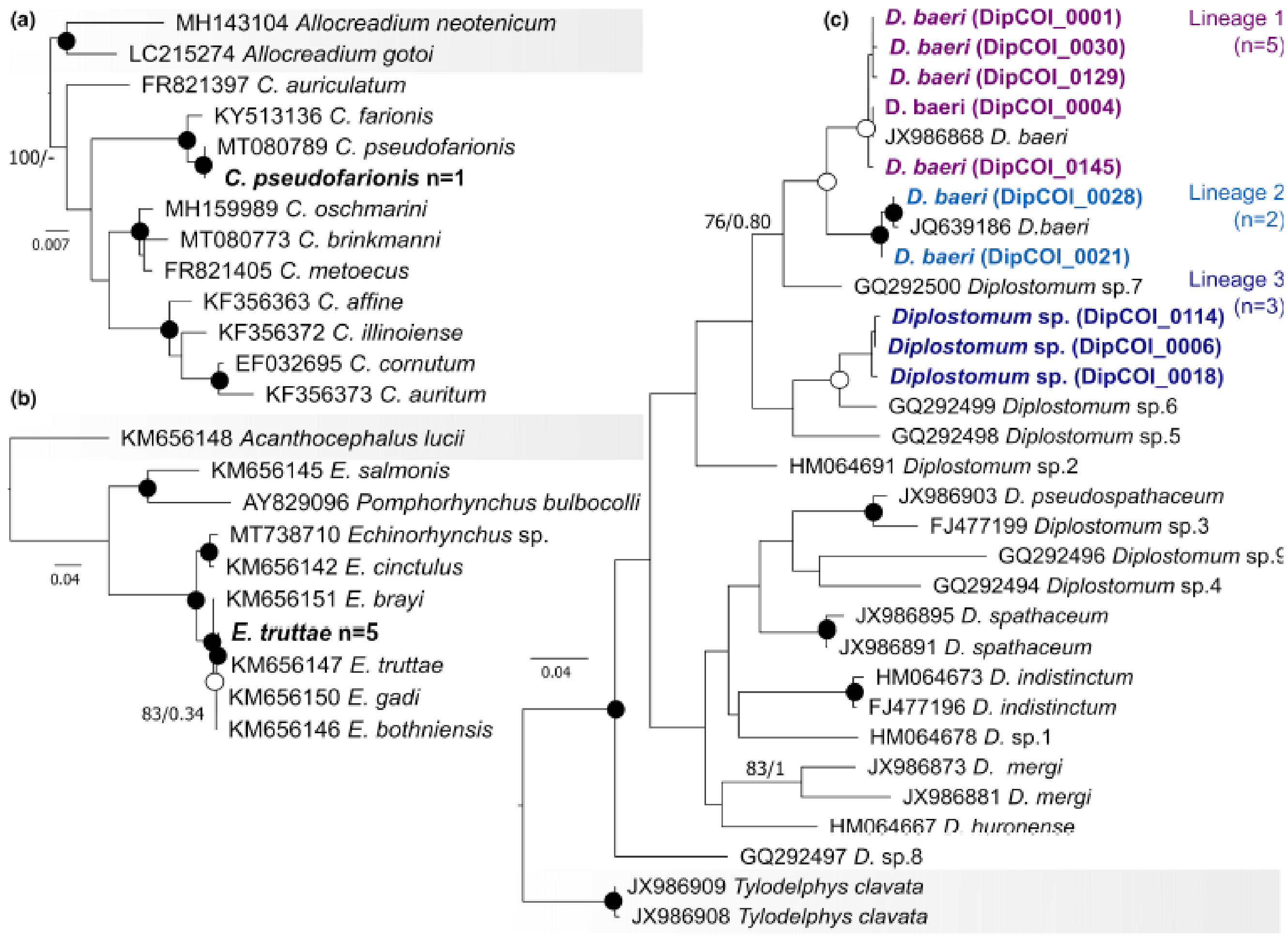

FIGURE 2 ML phylograms based on partial 28S rRNA or COI mtDNA (c) gene sequences of parasite specimens from this study and selected sequences from GenBank: (a) *Crepidostomum*, with three sequences of taxa belonging to *Allocreadium* as outgroup; (b) *Echinorhynchus*, with a sequence of *Acanthocephalus lucii* as outgroup; (c) *Diplostomum*, with two sequences of *Tylodelphys* as outgroup. Bootstrap values are followed by Bayesian posterior probabilities above the branches. Full circles at the nodes illustrate high support (ML> 90, BI = 1), and empty circles illustrate moderate support (ML = 70–90, BI = 0.90–0.99). Scale bars indicate the number of substitutions per site. Newly acquired sequences are marked in bold, and "*n*" indicates number of specimens sequenced.

parasite species richness did not vary between the morphs, but the total abundance of parasites increased with fish length (Table S2).

3.4 | Parasite infracommunities

A clear segregation between the parasite communities of the three Arctic charr morphs was found, despite some overlap between the planktivore and piscivore morphs (nonmetric multidimensional scaling analysis; Figure 3). The analysis had a stress value of 0.14, which fell within the accepted range (<0.2; Clarke et al., 2006). Additionally, these were supported by a significant difference (Adonis test; *p*-value = .001) in the parasite species composition and abundance in the infracommunities between the three morphs. The numerical vectors in the plot show that parasite infracommunities of the benthivore morph were mainly composed of nematodes (*P. salvelini* and an unknown nematode) and the GLM also showed a higher abundance of *P. salvelini* in this morph in contrast with the two other morphs, especially when compared to the planktivores that show the lowest abundance (*t* value = −2.6 and *p*-value = .011; Table S3). Parasite infracommunities of the planktivore morph were dominated by cestodes (*Dibothriocephalus* spp., *E. salvelini*, and *P. longicollis*; see Table 2) with a much higher abundance of *P. longicollis* than the other two morphs (*t* value = 4.7 and *p*-value <.001; Table S3). Piscivore-morph parasite infracommunities were driven by trematodes (*C. pseudofarionis*, *Diplostomum* spp. and *Tylodelphys* sp.; see Table 2) and acanthocephalans (*E. truttae* and *N. rutili*). Moreover, the abundance of autogenic parasite taxa (*Dibothriocephalus* spp., *Diplostomum* spp. and *Tylodelphys* sp.) was significantly linked with fish length (*Dibothriocephalus* spp. in piscivore: *t* value = 5.0 and *p*-value <.001; eye flukes in benthivore: *t* value = 2.6 and *p*-value = .011, and piscivore: *t* value = 2.3 and *p*-value = .021; Table S3).

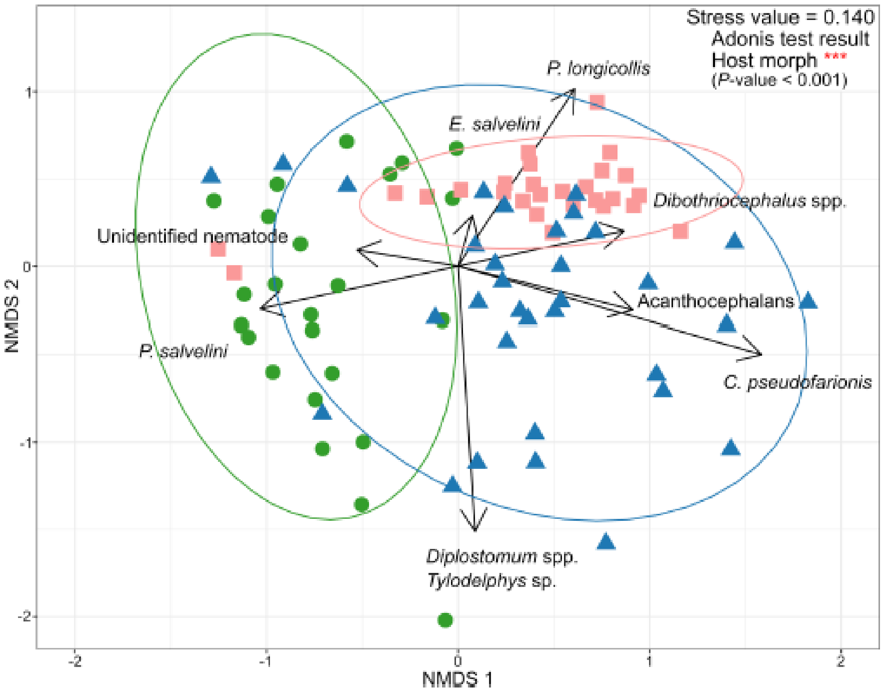

FIGURE 3 Nonmetrical multidimensional scaling biplot based on Bray–Curtis dissimilarity among parasite infracommunities ($N = 91$). Infracommunities are color-coded according to the host morph (green—benthivore morph; blue—piscivore morph; pink—planktivore morph). Ellipses regrouped 95% the parasite infracommunities of a particular host morph (colored accordingly). The vectors with arrows in black indicate the contribution of each parasite taxa to the dissimilarity. Random jitter (0.1) was added to the plot to improve visualization of overlapping data points. Asterisks represent p-values lower than .001 for the Adonis test results.

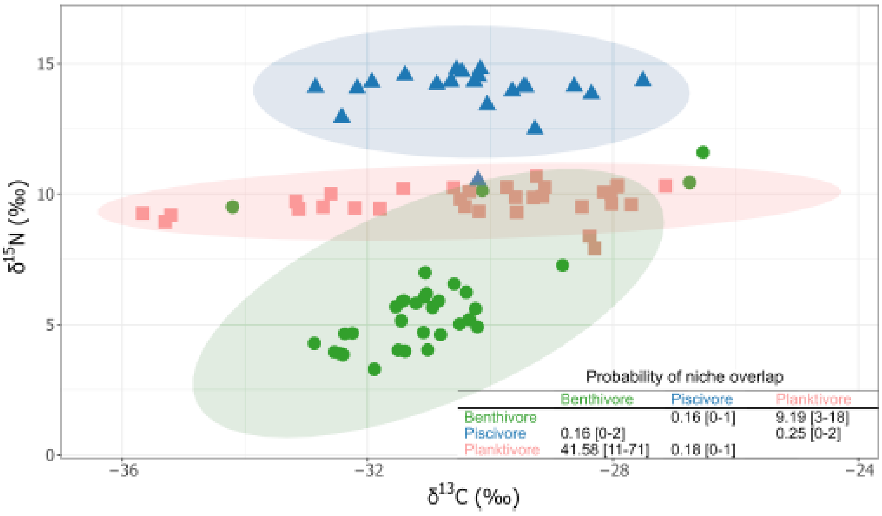

FIGURE 4 Plot of the stable isotopes $\delta^{13}C$ and $\delta^{15}N$ and probabilistic niche overlap calculated using the 95% niche regions between each pair of Arctic charr morphs from Loch Rannoch (2010). Colors refer to fish morph: green—benthivore morph; blue—piscivore morph; and pink—planktivore morph. Ellipses regrouped 95% of the fish of a particular morph (colored accordingly). Mean probability (%) (range 95% credibility interval) of finding an individual of the morph in the row within the niche region of the morph in the column.

3.5 | Stable isotope analysis

Our study was able to evaluate the temporal stability of polymorphic Arctic charr population, despite the limitation of our data, such as the absence of stable isotope data in 1992–93 and the smaller sampling effort in 2010. The stable isotope values showed clear separation of the three Arctic charr morphs mostly based on the $\delta^{15}N$ values (Figure 4; MANOVA: F-value = 225.23, p-value <.001) rather than the carbon signal. Indeed, there was no significant difference between the three morphs in $\delta^{13}C$ (MANOVA: F-value = 1.39, p-value = .255). Consistent with its diet, the piscivore morph displayed higher $\delta^{15}N$ (mean of 13.9 ± 1.0‰) values than the plankivore morph (mean of 9.7 ± 0.6‰), and the benthivore morph had the lowest $\delta^{15}N$ values (mean of 5.8 ± 2.0‰; Wilcoxon test: W-values = 671 and 1, p-values <.001; Figure 4).

The analyses of the isotopic niche overlap with $\alpha = 0.95$ suggested that the planktivore and benthivore morphs had the highest probabilities of sharing the same trophic region. The mean probability of an individual from the planktivore morph being found in the niche of the benthivore morph was 42 [11–71]% while there was a mean probability of 9 [3–18]% of finding a benthivore morph within the planktivore niche; Figure 4. The probability of either the benthivore or the planktivore morph trophically overlapping with the piscivore morph was low (<1 [0–1]% irrespective of the comparison base, e.g., Figure 4).

4 | DISCUSSION

Loch Rannoch Arctic charr morphs displayed high trophic niche stability over time. This is reflected in the consistent divergence in the parasite infracommunities and component communities' structure, diet composition, and stable isotope analyses of the three sympatric morphs. Overall, an increase in the prevalence (%) of all native parasite taxa in all three sympatric Arctic charr morphs was recorded between 1992–93 and 2010. Four novel macroparasite taxa were found in 2010, *C. pseudofarionis*, *P. longicollis*, *P. salvelini*, and an unidentified nematode. These parasites are generalist species commonly found as adults in salmonids, (e.g., Chubb, 1963; Dorucu, Crompton, et al., 1995; Moravec, 2004), thus they could have been introduced by the re-stocking of brown trout. The introduction of crucian carp may not be linked to the presence of these new taxa, as the only parasites are known to infect both crucian carp and Arctic charr are *Diplostomum spathaceum* (Rudolphi, 1819), *Acanthocephalus lucii* (Müller, 1776), and *N. rutili* (Karvonen et al., 2005). Moreover, it is unlikely that these parasite taxa were missed during the first study from Dorucu, Adams, et al. (1995), as the sampling in 1992–93 was larger than in 2010 and the relatively high prevalence of these new parasite taxa.

In our study, the piscivore morph had a low diet overlap with both the benthivore and planktivore morphs, which is consistent with earlier trophic studies in Loch Rannoch (Adams et al., 1998; Dorucu, 1996), and with other studies on similar charr-morph pairs (Knudsen, Gjelland, et al., 2016; Moccetti et al., 2019). The low diet overlap is supported by the distinct parasite infracommunity composition observed between the two sampling periods (Dorucu, Crompton, et al., 1995), and the markedly different stable isotope values for all morphs from 2010. The planktivore morph had a high diet overlap with the benthivore morph, mainly due to the high consumption of chironomid larvae by both morphs, and the relatively low consumption of zooplankton and copepods by the planktivore morph. The unexpected low zooplankton diet of the planktivore morph contrasted with earlier trophic studies in Loch Rannoch that showed >90% zooplankton in the planktivore diet (Dorucu, 1996; Walker et al., 1988). The difference may relate to the pooling of fish dietary data from October and July in the earlier study (Adams et al., 1998; Dorucu, 1996) and the use of October-only data in 2010. For example, seasonal abundances of zooplankton in Scottish lochs vary, being higher in June and July than in October (Romo, 1990). However, the high diet overlap between the planktivore and the benthivore morphs did not reflect their long-term niche divergence, as was indicated by time-integrated trophic tracers used here in the form of the parasite community and stable isotopes (mainly δ^{15}N values) analyses in 2010 that suggest highly diverged dietary niches over a period of several months. Altogether, our results confirm that the trophic niches are divergent between the sympatric morphs and seem to have remained relatively stable through time, i.e., over the 18 years between the two sampling periods used in this study. Similar trophic stability has been reported in other studies of lakes containing two and three sympatric morphs of Arctic charr (e.g., Knudsen et al., 1997; Knudsen et al., 2014; Siwertsson et al., 2016).

The planktivore morph was mainly infected with parasites transmitted by copepods, such as *P. longicollis*, *Dibothriocephalus* spp. and *E. salvelini*, as was noted in the earlier study of these morphs (Dorucu, Adams, et al., 1995). These parasite taxa are typically associated with other planktivore morphs of Arctic charr (Frandsen et al., 1989; Moccetti et al., 2019) and other salmonid species (Chubb, 1982; Knudsen et al., 2003). In addition to possible seasonal differences in availability, the relatively low occurrence of zooplankton prey in the planktivore morph diet could be linked to an introduced competitor of the planktivores such as juveniles crucian carp that feed on plankton (Penttinen & Holopainen, 1992), and juvenile native perch population that have increased in abundance in recent years (C.E. Adams personal com.). Moreover, Loch Rannoch is a relatively small water body and Arctic charr is a highly mobile species. Thus, the possibility of inter-specific interactions remains despite the potentially low abundance of crucian carp. Additionally, the sampling methods (i.e., time in the gillnets) can impact the occurrence of zooplankton prey in the planktivore morph, as zooplankton digestion will continue as long as the fish is alive in the gillnet. By contrast, infections of *P. longicollis* and *Dibothriocephalus* spp. were low in the benthivore morph (6 and 21%, respectively) suggesting a low consumption of zooplankton by this morph over time. The prevalent infection of *C. pseudofarionis* trematodes (23%) and *P. salvelini* nematode (39%) transmitted by insect larvae or amphipods and oligochaetes, respectively, were expected because the benthivore morph diet is apparently dominated by benthic prey.

Benthivore-specialized morphs of Arctic charr commonly have parasite communities that are clearly divergent from sympatric planktivore morphs (Moccetti et al., 2019; Siwertsson et al., 2016). The parasite community of benthivore morphs is mainly composed of taxa that use benthic species as intermediate hosts, such as snails, insect larvae, and amphipods (Knudsen et al., 2014). The divergence of the δ^{15}N stable isotope signals noted in this study corroborates the dissimilar parasite communities and the diet differences of the benthivore and planktivore morphs.

Parasite community studies of reproductively isolated piscivore morphs of Arctic charr are rare (but see Siwertsson et al., 2016; Moccetti et al., 2019). In Loch Rannoch, *E. salvelini* (52%) and *Dibothriocephalus* spp. (88%) show an increase in infection prevalence from 1992–93 to 2010. In agreement with previous studies, the diet of the piscivore morph consists mainly of fish, as supported by an elevated level δ^{15}N isotope in comparison to other morphs and the low niche overlap values (e.g., Knudsen, Amundsen, et al., 2016; McCarthy et al., 2004; Power et al., 2005). Additionally, a rather high prevalence of *C. pseudofarionis* (64%), *P. salvelini* (74%), and acanthocephalans (21%), all transmitted via benthic prey consumption, suggests that benthos (amphipods, oligochaetes, insect larvae) are also relatively common food items in piscivores and our finding corroborate previous observations (e.g., Moccetti et al., 2019).

There has been a general increase in infection levels of the native parasite taxa in all the Arctic charr morphs over time. In 2010, the eye flukes (*Diplostomum* spp. and *Tylodelphys* sp.) had the lowest infection in the planktivore morph, probably because the parasite larvae swarm from the *Radix* sp. snail populations in the littoral zone exposing the benthivore and piscivore morphs to highest infection pressures. The acanthocephalans (two species, Dorucu, Crompton, et al. (1995)) were infrequent in both time periods, mirroring a low feeding rate on *Gammarus*, the intermediate hosts for *E. truttae* and *N. rutili*. For the cestodes, *Dibothriocephalus* spp. and *E. salvelini*, prevalence increased distinctly between 1992–93 and 2010 for all morphs (up to 94%). Both these taxa can be transmitted to the fish host either by feeding on copepods directly or through feeding on fish prey (with parasite re-establishment in the predator). The increase in prevalence suggests altered transmission rates resulting from either change in the zooplankton community and/or the prey fish community. Re-establishment from prey fish explains the very high infection of these two parasite species in the piscivore morph in 2010, which were feeding intensively on fish.

The newly recorded parasite taxa (i.e., *C. pseudofarionis*, *P. salvelini*, *P. longicollis*, and the unknown nematode) in 2010 should be regarded as commonly occurring (prevalence up to 73%). These parasite taxa are easy to identify due to their distinct shape and size, and were unlikely to have been missed in the earlier 1992–3 study. *Proteocephalus longicollis* and *C. pseudofarionis* are common and relatively abundant in many salmonids, as well as in brown trout and Arctic charr (Moravec, 2004; Scholz & Hanzelova, 1998; Soldánová et al., 2017). Their presence is most likely attributed to the stocking of brown trout in the lake in previous years, with three of the new parasite species (i.e., *C. pseudofarionis*, *P. salvelini*, *P. longicollis*) known to infect different brown trout populations in the UK (Hartvigsen & Kennedy, 1993; Kennedy, 1978). None of these potentially introduced parasite species are regarded as problematic for Loch Rannoch Arctic charr. *Crepidostomum pseudofarionis* has not been previously reported as pathogenic for its final fish host (Moravec, 2004) and *P. longicollis* is usually not or only slightly pathogenic (Bauer et al., 1977; Moravec, 2001a; Scholz, 1999). Additionally, although capillariids are generally considered to be pathogenic at high infection levels, *P. salvelini* have not previously been reported as problematic (Moravec, 2001b; Moravec, 2004) and their abundances were generally low even in the most infected Arctic charr morph.

Arctic charr morphs in Loch Rannoch have shown an increase in parasite infections, as native parasite taxa have become more prevalent and new taxa have been established. Previous fish studies have shown relatively stable infection of trophic-transmitted parasite taxa through time (e.g., Kennedy, 2001; Kuhn et al., 2016). Changed transmission rates may have been caused by alterations in the food-web structure, for example, copepod transmitted parasites (Henriksen et al., 2019; Lopez & Duffy, 2021) related to human disturbances. In Loch Rannoch, one indirect cause of change could be the introduction of an alien fish species (e.g., crucian carp: Fraser & Adams, 1997) by fisherman and the increase in benthivore competitors (e.g., brown trout and perch), which may have altered the inter-specific competition between fish species and changed predator–prey relationships (e.g., Britton et al., 2010; Gregersen et al., 2006; Klemetsen et al., 2003), and thereby changed transmission rates and routes of parasites to the three Arctic charr morphs. As the parasite communities of crucian carp are very different from salmonids (Karvonen et al., 2005), it is unlikely that crucian carp and Arctic charr share parasite taxa. Introductions of fish or crustaceans have in many cases been shown to change lake ecosystems in the United Kingdom (Adams, 1994; Adams & Mitchell, 1992) but have also changed interactions between native sympatric species/morphs (Taylor et al., 2006) including Arctic charr morphs (Knudsen et al., 2019). Indeed, if the population of benthivore (e.g., crucian carp, brown trout, and perch) increases in future, it could affect the benthivore and planktivore morphs of Arctic charr. For instance, the introduced crucian carp predominantly feed on chironomid larvae and benthic cladocerans (among other benthic invertebrates) and could potentially compete with Arctic charr (Adams et al., 1998; Fraser & Adams, 1997; Penttinen & Holopainen, 1992). However, the introduction of crucian carp in the system should not be the main vector of the change in the parasite community of Arctic charr as they are not abundant in the lake (C.E. Adams pers.com). Alterations in the native fish community (e.g., trout stocking or increases in the perch population) may also initiate cascades in the food-web structure and Arctic charr niche (Sandlund et al., 2016). Then, the changes in the fish community might subsequently directly and indirectly change the parasite community structure of native (i.e., Arctic charr) fish hosts (e. g. Amundsen et al., 2013; Kelly et al., 2009; Kuhn et al., 2015). This change in the parasite community has also likely happened in the fish community of Loch Rannoch.

Overall, the Arctic charr populations in Loch Rannoch have lower infection levels of helminths compared with other northern lake systems (Amundsen et al., 2015; Kuhn et al., 2015; Paterson et al., 2018). Unfortunately, the intensity of parasite infections from the earlier study on Loch Rannoch system was not reported by Dorucu, Adams, et al. (1995), thereby preventing an assessment of the evolution of the parasite load through time. However, even if none of the potentially introduced species (i.e., *C. pseudofarionis*, *P. salvelini*, *P. longicollis*) are considered as highly detrimental to Arctic charr, the increase in infection of the native *Dibothriocephalus* spp. and *E. salvelini* may hamper growth and increase the negative impact at the individual or population level (Boyce, 1979; Curtis, 1984; Saksvik et al., 2001). Some piscivore and planktivore morph individuals from Loch Rannoch had *Dibothriocephalus* spp. infection intensities are known to have deleterious effects on Arctic charr elsewhere (e.g., inhibiting gonadal development; Curtis, 1984; Blanar et al., 2005). Given that Loch Rannoch supports the only known population of a piscivore morph of Arctic charr in Scotland (Adams et al., 1998; Gardner et al., 1988; Walker et al., 1988), an increased parasite load along with additional anthropogenic-induced stressors (e.g., fishing activity) could pose threats to the unique Arctic charr populations supported by this lake (Adams, 1994, 1996; Fraser & Adams, 1997).

In conclusion, the habitat, and the trophic behavior of the Arctic charr morphs in Loch Rannoch seem to be relatively stable through time. The parasite component communities remain distinct among the three Arctic charr morphs regardless of modifications to the fish community. However, the establishment of new parasite taxa (four species) and a general increase in infection load may represent altered negative effects on the local populations of Arctic charr morphs in the future.

AUTHOR CONTRIBUTIONS

Eloïse Coralie Rochat: Formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); project administration (equal); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Rachel Anne Paterson:** Formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Isabel Blasco-Costa:** Formal analysis (equal); methodology (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Micheal Power:** Investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Colin E. Adams:** Conceptualization (equal); data curation (lead); funding acquisition (supporting); project administration (equal); writing – original draft (equal); writing – review and editing (equal). **Ron Greer:** Data curation (lead); writing – review and editing (supporting). **Rune Knudsen:** Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

None declared.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.5061/dryad.jdfn2z3f2.

DATA AVAILABILITY STATEMENT

Data from the manuscript is publically available in the Dryad database (https://doi.org/10.5061/dryad.jdfn2z3f2). The DNA sequences will be submitted to Genbank (https://www.ncbi.nlm.nih.gov/genbank/).

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SUPPORTING INFORMATION

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Paper II

Parasite community re-assembly following eradication: is it predictable?

Authors

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Keywords

community resilience, recolonization, parasite eradication, salmonids, invasive species

Abstract

1- Ecological communities are initially formed through complex community assembly processes, and are shaped by factors such as environmental conditions and species interactions. Large-scale eradication events, whether natural or human-induced, provide unique opportunities to study community reassembly dynamics.

2- Data on Arctic charr (*Salvelinus alpinus* L.) and their parasite communities were collected from one control lake and two treated lakes (complete removal of fish populations) over a seven-year period, both before and after the treatment. The lake systems provide controlled environments to study the dynamics of parasite community re-assembly in response to a single eradication event of their fish hosts.

3- We identified 17 parasite taxa, revealing differences in infracommunity structure between lakes. The untreated lake maintained a stable parasite structure, while the treated lakes exhibited substantial changes and a gradual parasite community recovery/reassembly post-treatment.

4- The reassembly of parasite communities was influenced significantly by the dispersal abilities and life-history traits of the parasite species. Parasite taxa which utilize avian hosts were expected to rapidly recolonize the treated lakes; however, our results showed a more nuanced pattern of reassembly. Parasites with complex life cycle were the first back and the availability of their intermediate host through short-term disturbances facilitated their re-establishment.

5- Our study demonstrates that after large-scale disturbances, parasite communities can exhibit considerable resilience and complexity in their recovery patterns. These suggest that while some parasite species quickly reestablished, the overall community structure remained altered for a long time, with significant implications for ecosystem management and conservation strategies. This research shows the importance of long-term ecological studies for understanding the impacts of anthropogenic interventions on parasite dynamics and host-parasite relationships in freshwater ecosystems.

Introduction

Ecological communities consist of interconnected organisms that coexist within a defined space and time in natural environments or specific habitats (Townsend, 1989; Tilman, 1997). Over the years, ecologists have worked to understand and measure the importance of factors that drive species coexistence and diversity within these communities (Holt & Pickering, 1985; Tilman, 1997; Loke & Chisholm, 2023). Community assembly, which refers to the formation and development of communities (e.g. Swan & Brown, 2011; Aronson *et al.*, 2016), is influenced by various processes that determine species establishment, persistence or disappearance within a given ecosystem (Luh & Pimm, 1993; Bell, 2001). The assembly of a community is shaped by factors such as environmental conditions, species interactions, dispersal dynamics, and historical influences (e.g. Belyea & Lancaster, 1999; Marteinsdóttir & Eriksson, 2014). Understanding these complex drivers of community assembly is crucial for unravelling the complexities of ecological systems (Vellend, 2010; Nemergut *et al.*, 2013).

Large-scale eradication events, whether caused by natural disasters (e.g. Brook *et al.*, 2008) or human intervention (e.g. Theobald *et al.*, 2020), provide unique opportunities to observe the process of community reassembly from its inception. By closely studying these early stages of recovery, we can acquire important knowledge that not only enhances our understanding of ecosystem responses to future disturbances but also forms the basis for effective conservation and restoration strategies. The ability to predict how species interactions, population dynamics, and community structures respond to management actions is essential for making informed decisions in ecosystem conservation and restoration (Calizza *et al*., 2012; Meyer, 2014).

Acute disturbances often impact natural ecosystems by removing essential habitats (e.g. Ferrenberg *et al*., 2013; Friedman *et al*., 2017) and triggering competition for space (Connell & Slatyer, 1977). Previous studies focusing on community reconstruction after disturbances, such as mass eradication (e.g. wildfire: Ferrenberg *et al*., 2013; Gouezo *et al*., 2019) or disease outbreaks, can reveal the complexity and dynamics of community reconstruction (Jones *et al*., 2019). The initial phase of community reassembly often involves rapid colonisation by pioneer species which may include species that were previously present in the ecosystem, as well as the arrival of new species that can tolerate the altered environmental conditions (Belyea & Lancaster, 1999). Additionally, species with strong dispersal abilities tend to recolonize systems more rapidly than species with low dispersal abilities (Whitlatch *et al*., 1998; Cunillera-Montcusí *et al*., 2021). Over time, the impacted communities evolve along with ecological fluctuations, leading to changes in the relative abundance and diversity of each species (e.g. Best & Stachowicz, 2014). As a rule, less competitive species decline while more competitive ones thrive.

The study of parasite community reassembly differs from that of other ecological communities due to the unique relationship between parasites and their host populations (Lafferty, 2012). The dispersal capabilities dictated by parasite life history strategies and evolutionary constraints significantly impact community composition (Dobson, 1990). For instance, parasites with direct life cycles and those utilizing avian hosts (allogenic species) tend to be more successful invaders in aquatic ecosystems (Dobson & May, 1986). On the other hand, parasite species with complex indirect life cycles, requiring multiple host species throughout their development (e.g. autogenic species using exclusively aquatic host species), are highly dependent on the abundance and density of their intermediate host communities for their survival and persistence (Knudsen *et al*., 2007; Valtonen *et al*., 2010; Anderson & Sukhdeo, 2011) and are vulnerable to ecosystem disturbances (see e.g., Sures *et al*., 2023).

Moreover, there is a knowledge gap that hinders our ability to predict the long-term consequences of eradication events on communities (Myers *et al*., 2000). Specifically, we lack extensive, long-term studies that can shed light on how complex ecological communities, including both free-living and parasitic organisms, will respond to and recover from such interventions. While removing a given species is possible (e.g. Soleng *et al*., 2005; Adolfsen *et al*., 2021; Alfredsen *et al*., 2021), it can only be achieved under certain circumstances and may have unintended consequences for the community (Ballari *et al*., 2016).

This study gathered data on Arctic charr (*Salvelinus alpinus*) parasite infracommunities in three Norwegian lakes (two replicated experimental and one control lake) over seven years, both before and after a fish host eradication treatment. The primary objective of this research is to analyse the spatio-temporal patterns of parasite community re-assembly following the restocking of treated lakes with obligate juvenile fish hosts of local origin from parasite-free pisciculture facilities. The lakes selected for this study provide a unique opportunity to investigate the dynamics of parasite communities in discrete and comparable environments/ecosystems. Moreover, the untreated lake serves as a control as parasite community structure is relatively stable in undisturbed Arctic charr population through time (e.g. Rochat *et al*., 2022).

The study of parasite communities in freshwater ecosystems is essential due to their significant influence on fish health, population dynamics, and overall ecosystem stability (Poulin, 2007). Therefore, this research seeks to contribute to the existing body of knowledge on the recovery and resilience of parasite communities (i.e. ability of a parasite community to recover and maintain its structure, diversity, and function following disturbance or perturbation) following the removal of obligate fish hosts and their parasites (e.g. Lafferty & Kuris, 2005; Oros & Hanzelová, 2009; Strona, 2015). By studying the reassembly of parasite communities, insights can be gained into the mechanisms governing community dynamics and the potential impacts of eradication efforts on freshwater ecosystems. Additionally, understanding how parasites recolonize highly disturbed lake ecosystems can help identify the factors that drive the establishment and persistence of different parasite species.

Our study addresses the question of whether systems that have experienced large-scale disturbance events will regain their pre-disturbance parasite community structure and diversity. Furthermore, it provides valuable insights into the recruitment and re-establishment processes of parasites in host communities. We expect that the re-assembly of parasite communities in the treated lakes will be influenced by the dispersal abilities and life-history traits of different parasite species through time. In contrast, we expect that the parasite community structure will remain relative stable in hosts from the untreated lake. We hypothesise that allogenic parasite taxa will be the first invaders to rapidly recolonize the stocked juveniles fish hosts in both treated lakes. Moreover, we hypothesise that the community composition of parasitic species seven years after treatment disturbance will still differ from the pre-treatment community structure with fewer taxa. We test these hypotheses by comparing the parasite infracommunity structure in Arctic charr hosts through time from two treated lakes (downstream) and an untreated lake (uppermost) in the same catchment that serves as a control location.

Material and Methods

Study area

The study was carried out in three oligotrophic lakes: Luktvatnet (3.8 km^2; 137m above sea level (masl)), Ømmervatnet (5.6 km^2; 42 masl) and Fustvatnet (10.6 km^2; 39 masl) in northern Norway. The lakes are all in the Fusta catchment (544 km^2) and connected to Vefsn fjord by the Fusta river (Hytterød *et al*., 2011; Paterson *et al*., 2018). Before 2012, the fish communities in this catchment were composed of landlocked Arctic charr with genetically distinct populations residing in each lake (Præbel & Knudsen, 2012a; Præbel & Knudsen, 2012b), both landlocked and anadromous (only in the lower lakes) brown trout *Salmo trutta* L., three-spined stickleback *Gasterosteus aculeatus* L., in addition to a small population of European eel *Anguilla anguilla* L (Hytterød *et al*., 2011). Moreover, Atlantic salmon *Salmon salar* L. were potentially present in the lakes (except uppermost Luktvatnet) until 1992 when the fish ladder on Fusta river was closed down (Sæter, 1995). The fish ladder was closed throughout the whole study period. However, anadromous brown trout were moved past the fish ladder manually in the period from 1992 to 2000 and then in 2008 and 2009 (H. Hansen pers. comm.).

In 2010, the monogenean *Gyrodactylus salaris* (Malmberg, 1957), an invasive ectoparasite of wild salmonids was detected on Arctic charr in three of the four lakes of the Fusta catchment (Ømmervatnet, Mjåvatnet and Fustvatnet) (Hytterød *et al*., 2011). This parasite caused major losses by negatively affecting salmon health and increasing mortality rates (e.g., up to 98% Adolfsen *et al*., 2021).

Prior to the eradication treatment, egg and semen of each lake's population of Arctic charr and brown trout were taken and bred separately in a fish hatchery for future fish restocking. In Autumn 2012, lakes Ømmervatnet, Mjåvatnet and Fustvatnet were treated with the piscicide rotenone to eradicate *G. salaris* (Hanssen, 2013). Luktvatnet was not treated as *G. salaris* was not reported there and serves as a control site in our study. Indeed, *G. salaris* with its direct life cycle (one host) is vulnerable to extinction if its hosts are killed. After the treatment, the fish communities from Ømmervatnet and Fustvatnet died and also the macroinvertebrate community was negatively affected by the treatment (e.g. Kjærstad *et al*., 2022). Subsequently, Arctic charr locally adapted from each lake and brown trout were first reintroduced to the lakes in late autumn 2013 (only few individuals) and spring 2014 (Kjærstad *et al*., 2019).

Samples collection

Arctic charr (n = 3-33, see Table 1) were sampled each year using two techniques in all three lakes (Fustvatnet, Ømmervatnet and Luktvatnet). Each lake was sampled prior to treatment initiation (referred to as "Before Treatment") and subsequently after the treatment had been implemented (referred to as "After Treatment"). Sixty dead fish were collected in 2012 during the rotenone treatment in Fustvatnet and Ømmervatnet (data used in Paterson *et al*., 2018). All the other fish were sampled using a benthic gill net in 2010, 2012 (Luktvatnet only), 2014/2015, 2017, 2018 and 2019 in each lake. The number of fish sampled in the treated lakes varied in 2014 and 2015 (see Table 1) because of the recent fish restocking. The fish from Mjåvatnet were excluded from this study because it is a shallow lake and thus was less suitable habitat for charr. Moreover, Mjåvatnet is only separated from Fustvatnet by a narrow headland, and thus can be considered an extension of that lake. Upon capture, fish were measured (fork length; including fish of 110 to 392 mm with an average length of 243.4 SE 2.2 mm), weighed (g) and aged (using otoliths). All the fish sampled were killed following the strict codes of practice in force in Europe. The fish were frozen at -20°C, transported to the laboratory and a standardized examination was conducted to collect data on parasite infracommunities. This included the collection and identification of individual parasite specimens, as well as quantification of their abundance (total number of individual parasites of a species per host individual) and prevalence.

Parasite identification

The fish sampled between 2010 to 2019 were examined for metazoan parasites from their organs under a stereomicroscope. We only investigated a subset of kidneys for the presence of Myxozoans and thus, Myxozoans were excluded from further analyses. Moreover, only the right eyes of each fish were examined for parasites. The use of frozen samples in our study could have led to a slight underestimation of monogenean abundance. Indeed, small monogeneans like *Gyrodactylus* tend to be harder to find on frozen hosts. However, we were consistent throughout the study and only used frozen specimens. Parasites were fixed in absolute ethanol for further morphological and molecular analyses. Specimens used for the morphological analyses were whole mounts (Cribb & Bray, 2010; Justine *et al*., 2012) and they were identified using external taxonomical criteria (e.g. Moravec, 1994; Moravec, 2004).

Molecular data were obtained from a subsample of specimens for each prospective parasite taxa to confirm their morphological identification. The DNA extraction, PCR amplification of the large ribosomal subunit (28S rDNA) and small ribosomal subunit (18S rDNA) following the protocol as in Rochat *et al.* (2022). Additionally, a cytochrome c oxidase subunit I mitochondrial gene (COI) was also amplified using specific primers depending on the targeted parasite genus (JB3 and trem.cox1.rrnl or Plat-diploCOX1hF and Plat-diploCOX1R). The PCR amplification for the COI gene, the PCR reaction mixture consisted of 15 µl, with 3 µl of DNA template, 7.5 µl of 2x MyFiTM (enzyme from Bioline France 2017), 1.8 µl of deionized water, and 0.6 µl of each forward and reverse primers, resulting in a final concentration of 4 pmol/µl. The PCR reactions ran for 35 cycles, including denaturation at 94 °C for 50 s, annealing at 45 °C for 50 s, and extension at 72 °C for 60 s. The 35 cycles were preceded by an initial denaturation at 94 °C for 3 min and followed by a final extension of 72 °C for 10 min. Purified amplicons were sequenced by Macrogen Europe (Amsterdam, Netherlands) using the same primers as for PCR. Then, the sequencing analysis and phylogenetic analysis were carried out as in Rochat *et al.* (2022). Note that the parasite from 71 fish sampled in 2012-2013 were molecularly analysed by Paterson *et al.* (2018). All the sequences generated in the study are deposited in GenBank® (accession numbers in Supplementary Table S1).

Statistical analyses

Two infection parameters, i.e. parasite prevalence (i.e. the proportion of individuals infected in a host population) and mean abundance (i.e. mean number of parasites per host), were calculated for each parasite species (Bush *et al.*, 1997). All analyses were carried out on the parasite infracommunities of 402 Arctic charr and performed with the statistical software R version 4.2.2 (www.r-project.org). Our dataset included information on individual fish (age, length, residual weight) for each lake and year, and the parasite species and their abundance in each fish.

The dissimilarity among the parasite infracommunities through time as a function of the lake was assessed by using the multidimensional scaling ordination method (MDS) *stat::cmdscale* (R Core Team, 2021). The species abundances were standardized using the function *vegan::decostand* (Oksanen, 2015). The Bray Curtis distance was used to create the distance matrix needed for the MDS computation. This technique provided a graphical representation of the dissimilarity in parasite community composition, allowing for visual assessment of temporal and treatment-related trends. The MDS representation was exported and further edited in Inkscape v1 for better visibility. Taxa that were rarely represented in the parasite communities (overall prevalence in the dataset or subset data below 5%) were excluded from this analysis. Additionally, a permutational multivariate analysis of variance (PERMANOVA) was carried out to test for significant differences in parasite community structure between lakes and over time using the Adonis function *vegan::adonis2* (Oksanen, 2015). Then, three additional Bray Curtis distance matrices and MDS were computed using the subset data of each lake to analyse their parasite infracommunity. The variances in abundance within each distance matrices were analysed using another PERMANOVA *pairwise.adonis2::pairwiseAdonis* (Martinez Arbizu, 2020). This pairwise comparison enabled the evaluation of group differences in a pairwise manner.

The distribution and abundance of multiple parasite species within the Arctic charr host population, between the lakes and within each lake, were then simultaneously analysed using Joint Species Distribution Modeling (JSDM). This statistical approach is well-suited to assess the relationships between species, environmental covariates, and treatment effects. Here, the JSDM was performed using *mvabund* package (Wang *et al*., 2012), which provides the *mvabund::manyglm* function for fitting multivariate generalized linear models (GLMs) and Poisson distribution to ecological count data. Moreover, the data from 2014 and 2015 were pooled together for the analyses of the parasites' abundance in Fustvatnet and Ømmervatnet (treated lakes) because of the small sample size. Moreover, the years, host length and residuals weight were used as predictor variables. The choice between using host length or age in the JSDM model was based on the Akaike Information Criterion (AIC); the model with the lower AIC is generally considered better, as it strikes a better balance between goodness of fit and model complexity.

Additionally, the differences in parasite prevalence and mean abundances over time were assessed in each lake with a Chi-square test for all the species at the component community level (i.e. all the infracommunity of parasites associated with a subset of a host species). Then, variation in the parasite species' commonness and rareness was analyzed over time in each lake. The data were sorted and the probability of each species being common was computed with confidence intervals using the following functions *FuzziQ::fuzzyq*, *FuzzyQ::fuzzyqBoot* and *FuzziQ::fuzzyqCI* (Balbuena *et al*., 2021).

Results

Parasite fauna and communities across all lakes

In our study, we identified a total of 17 parasite taxa through a combination of morphological and genetic analyses. Among these, 12 taxa were identified to species, while the remaining five were identified to genus level (see Table 1). The parasite infracommunities showed some differences through time in structure between the three lakes (Adonis2: F-value = 13.05, *P*-value = 0.001, Figure 1, Supplementary Table S2). These differences are mainly reflected in the presence or absence of the rare species (see Table 1).

Parasite infracommunity of the control (untreated) lake

The parasite communities in Luktvatnet comprised 12 parasite taxa, including four rare taxa, and was relatively stable through time with an average of nine species found every year (Table 1). Moreover, low-prevalence species such as *Apatemon gracilis*, *Contracaecum* sp., *Pseudopapillaria salvelini*, and *Salmonema ephemeridarum* were not consistently found every year and considered rare in Luktvatnet (see Table 1). The abundances of allogenic and autogenic species were stable over time (Figure 2). However, it was noteworthy that the presence of certain species fluctuated over time (Figure 3). The prevalence and commonness index of *Eubothrium salvelini* and *Proteocephalus* sp. increased in 2015 and 2019 (Chi-square: *X*-value = 169.95, *P*-value < 0.001, Supplementary Table S3 & Figure 3). *Salmincola edwardsii* were present in Luktvatnet every year at a prevalence between 13-30% and this is a distinct feature of this lake (Table 1). Some variations are also observed in the parasite infracommunity structure (see Supplementary Table S4 & S5) but parasite abundances did not vary over time (see the JSDM results in Supplementary Table S6). Furthermore, allogenic and autogenic parasite abundances appeared to be predominantly influenced by the length of the sampled fish as bigger fish have more parasites than smaller fish (GLM: host length: *T*-value = 3.19, *P*-value = 0.002; see Supplementary Table S7). Allogenic parasites were less abundant in 2015 and 2019 than in 2010 (GLM: 2010-12 VS 2015: *T*-value = -2.34, *P*-value = 0.020; 2010-12 VS 2019: *T*-value = -2.31, *P*-value = 0.022; Supplementary Table S7). Then, autogenic parasites were more abundant in 2014, 2015 and 2019 than in 2010-12 (GLM: 2010-12 VS 2014: *T*-value = 2.44, *P*-value = 0.016; 2010-12 VS 2015: *T*-value = 2.39, *P*-value = 0.018; 2010-12 VS 2019: *T*-value = 2.49, *P*-value = 0.014, Supplementary Table S7).

Parasite infracommunities of the treated lakes

The two treated downstream lakes, Fustvatnet and Ømmervatnet, exhibited diverse parasite infracommunities prior to the rotenone treatment. The lakes shared 14 parasites species in 2010-2012, with a higher species abundance in Fustvatnet than in Ømmervatnet, except for *Phyllodistomum umblae* (14 taxa shown in Table 1, as previously reported by Paterson et al., 2018). Fustvatnet harboured a high number of parasite taxa, including the most common species such as three allogenic parasite taxa (*Dibothriocephalus* spp., *Diplostomum* sp. and *Tylodelphys* sp.) and two autogenic parasites (*Pseudocapillaria salvelini* and *P. umblae*). The most common species in Ømmervatnet are three allogenic parasites as in Fustvatnet in addition to two autogenic species (*E. salvelini* and *P. umblae*). Notably, the two treated lakes harboured a higher number of taxa and individual parasites compared to the control lake in the upper catchment (Luktvatnet, Table 1). For example, monogeneans and two nematode species (*P. salvelini* and *Contracaecum* sp.) were exclusively recorded in the two lower lakes, and *Tetraonchus* sp. was found only once in Ømmervatnet.

Following the eradication treatment, a substantial reduction was observed in the parasite infracommunities of Fustvatnet and Ømmervatnet, reflected in species composition, abundance, and prevalence (Table 1). The parasite prevalences in fish decreased for most of the taxa just after the treatment (i.e. 2014 - 2015) before it increased again (Chi-square Fustvatnet: X-value = 1376.1, *P*-value < 0.001 ***; Chi-square Ømmervatnet: X-value = 711.98, *P*-value < 0.001), except for *Crepidostomum* spp. and *S. ephmeridarum* that became more prevalent in the year following the treatment, even after seven years.

The commonness of the parasite species was influenced by the eradication treatment. The commonness of autogenic trematodes increased post-treatment (years 2014-15) in both the treated lakes, with *Diplostomum* sp, *P. umblae* and *Crepidostomum* spp. being the most common parasites followed by *P. salvelini* in Fustvatnet (Figure 3). Later the commonness of the trematodes stayed high also compared to the pre-treatment condition, except for *Crepidostomum* spp. with gradually decreasing commonness index in later years (Figure 4). On the contrary, commonness of the allogenic cestode (e.g. *Dibothriocephalus* spp.) showed an opposite pattern. The commonness index decreased during the two-first years post-treatment before increasing again over the years (Figure 4).

These changes in commonness were reflected in the abundance of allogenic and autogenic parasites. The abundances of autogenic and allogenic parasites drastically decreased after the treatment in the two lakes. In Fustvatnet, the allogenic parasites were less abundant in years 2014-2015-2017 post-treatment, however by 2019 no difference with respect to 2012 in the abundance of allogenic parasites was noted (see the GLM results in Supplementary Table S8; Figure 2). In Ømmervatnet, we observed significantly fewer autogenic parasites after the treatment, even 7 years later (see the GLM results in Supplementary Table S9; Figure 2), and more allogenic parasites than before the treatment. Moreover, the abundance of autogenic and allogenic species did not vary significantly among the post-treatment years (Supplementary Table S9).

Significant alterations in infracommunity structure were also observed between years for Ømmervatnet (Adonis2: *F*-values = 8.48, *P*-value = 0.001; Supplementary Table S10) and Fustvatnet (Adonis2: *F*-values = 26.16, *P*-value = 0.001; Supplementary Table S11). Indeed, a clear shift was observed in the parasite infracommunity structure between the pre-treatment phase and two years post-treatment in Fustvatnet and Ømmervatnet (Figure 1). Then, the parasite infracommunities changed over time and the mean of the parasite infracommunities in 2019 got relatively close to its pre-treatment mean in 2010-12 (see the pattern drawn by the arrow in Figure 1 and Supplementary Table S12 & 13). Moreover, the fish parasite infracommunities were changing every year except the two last years in Fustvatnet (pairwise.adonis2: *F*-values = -23.82, *P*-value = 0.630; see Supplementary Table S12).

The variance of the parasite infracommunities was strongly associated with the length of the host as bigger fish can accumulate more parasites (see JSDM results in Supplementary Table S14 and S15). We observed significant changes in the infracommunity variance associated with the year of sampling. Fustvatnet infracommunity variance was different in 2019 and Ømmervatnet showed a higher variance in 2017 (JSDM e.g. ØM 2010-12 vs 2017: Wald value =17.64, *P*-value = 0.008; Supplementary Table S 14 & S15).

Discussion

Our study showed an almost complete re-assembly of the parasite communities following the total eradication of the obligate fish hosts and their parasite infracommunities. This sheds light on the complex dynamics but also resilience of these parasite communities in freshwater ecosystems. Following the eradication treatment, there was a substantial reduction in parasite infracommunities in the treated lakes, reflected in changes in their species composition, commonness, abundance, and prevalence. One main driver of the re-establishment of parasite taxa seems to be linked with the parasites surviving in invertebrate intermediate hosts and birds. In contrast, we observed a relatively stable community structure over the same time period in hosts from the uppermost control lake, as expected. Additionally, as we hypothesized the parasite community composition seven year after treatment disturbance was still different from the pre-treatment community structure.

Contrary to our hypothesis, allogenic parasite taxa were not the first to recolonize the restocked native hosts in the two treated lakes. Autogenic trematodes were quick to re-establish in their fish host. The main re-establishment factor appears to be the larval trematode survival in intermediate mollusc hosts and to a lesser degree the infections of adult stages in birds that persisted regardless of the treatment. Accordingly, our results showed more of a species-specific pattern of re-establishment instead of distinct allogenic versus autogenic recolonization. This outcome contrasts with other studies highlighting the advantages of allogenic species in colonization from one locality to another (e.g. Esch *et al*., 1988; Criscione & Blouin, 2004; Marcogliese, 2005). Thus, species that are best at colonizing new locations (due to their highly mobile hosts) are not necessary ’best’ at surviving ecosystem disturbances. This suggests that most parasite taxa in our system exhibit a robust ability to re-establish in the host population or survive in their other (intermediate) hosts and gradually rebuild their populations over time following disturbances.

Parasite taxa with a simple life cycle (i.e. monoxenous) showed a weaker ability to recolonise the reintroduced host than parasites with a complex life cycle (i.e. heteroxenous). For instance, the prevalence of *Salmincola edwardsii* declined in the two treated lakes but remained stable in the control lake. Additionally, two monoxenous taxa (i.e. *Gyrodactylus salaris* and *G. salmonis* see Mo *et al.* (2023)) have disappeared from the systems (Veterinærinstituttet, 2024), demonstrating the efficacy of the eradication treatment against monoxenous parasites of fish. This result was expected as the target of this eradication campaign was *G. salaris* (Adolfsen *et al*., 2021). However, this outcome differs from previous studies that showed that monoxenous parasites are less sensitive to stressful environments compared to parasite taxa with complex life-cycles (Sures *et al*., 2023 and references therein).

Our results suggest that parasite taxa with complex life cycles may persist in the ecosystem (i.e. in intermediate hosts) during short-term disturbance. This contrasts with the findings by Wood *et al.* (2023) that show complex life cycles to be more vulnerable to long-term environmental changes than parasite taxa with simple life cycles. One explanation could be that heteroxenous parasites can maintain their life cycles (for a period of time) in rotenone-resistant invertebrate intermediate hosts, while the fish host is removed from the ecosystem. This is supported by cases of allo- and autogenic trematodes with complex life cycles and a molluscan intermediate host, which appear minimally affected by rotenone treatment and can quickly repopulate (e.g. Chandler & Marking, 1982; Holcombe *et al*., 1987; Arnekleiv *et al*., 1997;

Kjærstad & Arnekleiv, 2011; Kjærstad *et al*., 2019). In contrast, cestodes that rely on copepods as their first intermediate host show a delayed return in restocked fish, likely due to the high impact of rotenone treatment on copepods which disappear from the treated lakes in 2013-14 (Kjærstad *et al*., 2019). This highlights that life cycle complexity and intermediate host resilience determine the parasites' ability to withstand ecosystem perturbations. Interestingly, the nature of the first intermediate host, whether molluscs or copepods and their sensitivity to the treatment, seems to play a driving role in determining the speed of parasite recovery after the eradication than whether part of the life cycle occurs outside the aquatic habitat. This observation also agrees with the difference in sensitivity to pollution observed between trematodes and cestodes (Poulin, 1992).

An alternative explanation to the survival in the intermediate hosts could be the influx of parasites (i.e. fish or infected intermediate hosts) from untreated parts (e.g. our control lake) of the catchment area. Trematodes and cestodes differ in their transmission pathways and physiology. Some trematodes species are generalist, e.g. *Crepidostomum* spp., and can infect other freshwater salmonids (Moravec, 2004; Paterson *et al*., 2018; Faltýnková *et al*., 2020), including brown trout that were also restocked in the treated lakes (Kjærstad *et al*., 2019). Thus, trematode re-establishment could be facilitated by the more mobile brown trout alternative host (Præbel & Knudsen, 2012) dispersing from the untreated lake. In comparison, two of the cestodes in our system (e.g. *Eubothrium salvelini* and *Proteocephalus* sp.) tend to be more host-specific to Arctic charr and were slower to e-establishing in the treated lakes (Moravec, 2004; Brabec *et al*., 2023). *Dibothriocephalus* spp., on the other side can use other salmonid and three-spined stickleback as intermediate hosts and fish-eating birds as final hosts (Waeschenbach *et al*., 2017), which can facilitate their return to treated lakes. Three-spined sticklebacks were not restocked after the fish eradication but immigrated from brooks and ponds in the catchment. This indicates a species-specific response to disturbance events with parasite survival in intermediate hosts being a key factor, emphasizing the importance of understanding the intricacies of parasite life cycles (Blasco-Costa & Poulin, 2017) and specific water system to predict community reassembly dynamics.

Our results also underscore the concept of community stability. The control lake, which did not undergo eradication treatment, exhibited a consistent parasite community structure, reaffirming the stability inherent in undisturbed ecosystems in preserving their community composition. This relative stability of an undisturbed systems was previously observed in several studies, including in Arctic charr (e.g. Kuhn *et al*., 2016; Rochat *et al*., 2022). Moreover, the stability of the control lake may have contributed to the resilience of the lower treated lakes.

The presence of mobile species in the systems (Folke *et al*., 2004), coupled with the capacity to facilitate the recolonization of parasite communities in treated lakes can be substantial (e.g. Lafferty & Kuris, 2002). Mobile species, such as migratory fish or birds, serve as vectors for parasite dispersal between nearby lakes (e.g. Johnson & Hoverman, 2012). As a result, neighbouring lakes with intact parasite communities may act as reservoirs, potentially supplying parasites to treated lakes undergoing restoration or recovery from disturbance (e.g. Krkošek *et al*., 2005). Our data shows that the ecological connectivity between undisturbed and treated water bodies, facilitated by mobile species that link different ecosystems, may allow for an exchange of parasites, helping the stability of the recovering ecosystems. This highlights the importance of considering the specific life cycle and dispersal capabilities of parasites in predicting community reassembly dynamics. Additionally, it also participates to our understanding of the factors (e.g. host dependency, re-establishment process) driving the establishment and persistence of different parasite species in treated lakes (Runghen *et al*., 2021).

Our results provide intriguing insights into the intricate dynamics between parasites and host populations during community recovery and reassembly following an eradication event. The initial phases of reassembly, characterized by the rapid establishment of pioneer species, align with existing ecological theory (e.g. Connell & Slatyer, 1977; Walker & Del Moral, 2003; Budischak *et al*., 2016). The complexity of parasite-host interactions and their responses to disturbances becomes evident in the temporal differences in the composition of hosts available for re-establishment (Gunderson & Pritchard, 2012). Initially, our findings suggest that after the treatment, the specific characteristics and resilience of the intermediate hosts can lead to variability and unpredictability in the reassembly and distribution of parasite species in the ecosystem. As time progresses, deterministic processes become more influential, implying that certain factors or rules start to govern the community structure, resulting in a more ordered and predictable pattern of species distribution, reflecting patterns seen in free-living taxa (e.g. Sarà *et al*., 2006; Wanner *et al*., 2008; Martins *et al*., 2018). Not only did the parasite community composition change, but alterations in parasite abundances were also strong, emphasizing the intricate interplay between parasites and their host populations. The life-cycles of parasites in a typical community in sub-arctic lakes generally involve many different hosts (e.g. Amundsen *et al*., 2009) and altered parasite communities can reflect ecosystem changes (Marcogliese, 2005). Therefore, the parasite community's reassembly in our case suggests that the whole aquatic community could recovers and performs relatively stable through time.

The long-term consequences of eradication efforts on community structure, as observed in the differences between treated (Fustvatnet and Ømmervatnet) and untreated (uppermost Luktvatnet) lakes, show the need for comprehensive, long-term studies. The persistence of some alteration in Ømmervatnet community composition showed the vulnerability of aquatic ecosystems to the eradication of top predators and their impact on trophic networks (Carpenter *et al*., 2001; Carpenter, 2003). However, the parasite community in Fustvatnet in 2019 shows a return close to its pre-disturbance states, suggesting a potential for near-complete recovery in Ømmervatnet too. This highlights the role of environmental factors in guiding community convergence (Caro *et al*., 2010). These results further emphasize the complexity of parasite community reassembly following significant disturbances and underscore the importance of long-term monitoring in treated ecosystems.

Our finding have important implications for ecosystem management strategies, demonstrating the lasting impacts of rotenone eradication treatments in order to successfully eradicating an ectoparasite, *Gyrodactylus salaris* (Veterinærinstituttet, 2024). Nevertheless, the rotenone treatment, while targeting specific parasites, indirectly impacted other monoxenous parasite taxa and overlooked those transmitted by invertebrates, which were also potentially affected (Donnelly, 2018). This treatment has long-term effects on invertebrate communities (Kjærstad *et al*., 2022a; Kjærstad *et al*., 2022b), which in turn influences parasite communities both directly and indirectly. Although some parasite taxa managed to recolonize and re-establish, others did not return within the study period. Moreover, based on the present study, the rotenone treatment has likely affected the fish host populations (restocked F1-generation) and therefore the host parasite interactions. This eradication treatment may induce a loss or alteration of genetic diversity of salmonid hosts (e.g. genetic bottleneck effect, Bakke *et al*., 2004) and general trophic diversity (Eloranta *et al*., 2022). The eradication of key functional groups from an ecosystem can also alter the ecosystem resilience and induce more vulnerability to future disturbances (Chapin *et al*., 1997; Luck *et al*., 2003).

In conclusion, our study contributes new insights into the re-establishment and resilience of parasite communities' post-eradication of obligate fish hosts and their parasites in freshwater ecosystems. In contrast with the invertebrate community that may recover within one year (Vinson *et al*., 2010; Woods *et al*., 2016; Beaulieu *et al*., 2021), parasite communities showed a longer recovery period. The observed taxon-specific patterns in re-establishment, along with the resilience of the parasite community structure and the complexities of species interactions, emphasize the importance of long-term monitoring. Moreover, our results revealed a relative high degree of resilience for parasite communities with complex life cycles, regardless of autoor allogenicity, following short perturbation events. This underscores the need for a comprehensive understanding of ecological drivers to predict the dynamics of community reassembly. Such insights are essential for informed decision-making in ecosystem conservation and restoration, especially help us to better predict how host-parasite communities are responding to large-scale disturbances and eradication events.

Table

Table 1: Infection parameters for the parasite community from three lakes (control lake: Luktvatnet and treated lakes: Ømmervatnet and Fustvatnet) in the Fusta catchment, Norway, expressed as the prevalence of infection (%) and mean abundance (±SE) before and after an eradication treatment (fall 2012). The data on 72 Arctic charr from 2012 published by Paterson et al. (2019) were included in this study. Asterix indicate the autogenic (*) or allogenic (**) life cycles used by each parasite species.

Parasite taxa		**Luktvatnet**				**Ømmervatnet**						**Fustvatnet**					
		2010-2012	2014	2015	2019	2010-2012	2014	2015	2017	2018	2019	2010-2012	2014	2015	2017	2018	2019
N =		30	30	31	30	32	3	9	22	33	33	30	5	22	30	30	32
Monogenean																	
Tetraonchus sp.	*	-	-	-	-	**3.0** 0.03 (0.03)	-	-	-	-	-	-	-	-	-	-	-
Discocotyle sagittata	*	-	-	-	-	12.1 0.1 (0.06)	-	-	-	-	-	**53.3** 1.3 (0.3)	-	-	-	-	-
Trematoda																	
Diplostomum sp.[a]	**	**100.0** 37.5 (4.1)	**100.0** 18.2 (3.5)	**100.0** 23.0 (2.1)	**100.0** 30.6 (9.5)	**97.0** 18.3 (3.3)	**66.7** 1.0 (0.6)	**90.0** 10.1 (4.1)	**100.0** 17.3 (5.6)	**100.0** 11.5 (1.1)	**100.0** 11.9 (2.3)	**100.0** 200.8 (30.2)	**100.0** 11.4 (4.3)	**100.0** 9.4 (1.1)	**100.0** 21.8 (2.2)	**100.0** 51.7 (7.4)	**100.0** 70.8 (10.0)
Tylodelphys sp.[a]	**	**33.3** 1.1 (0.4)	**13.3** 0.2 (0.1)	**38.7** 0.5 (0.1)	**16.7** 0.3 (0.1)	**63.6** 3.4 (0.8)	-	**20.0** 0.3 (0.2)	**59.1** 1.1 (0.2)	**39.4** 0.6 (0.2)	**39.4** 1.3 (0.4)	**100.0** 31.4 (5.3)	**60.0** 0.8 (0.4)	**18.2** 0.2 (0.1)	**33.3** 0.6 (0.2)	**33.3** 1.5 (0.5)	**68.8** 2.4 (0.6)
Apatemon gracilis[a]	**	-	-	**3.2** 0.03 (0.03)	-	-	-	-	-	**3.0** 0.03 (0.03)	**9.1** 0.1 (0.1)	-	-	-	-	-	**3.1** 0.1 (0.1)
Phyllodistomum umblae	*	**100.0** 60.5 (6.0)	**100.0** 77.7 (5.5)	**100.0** 75.2 (7.6)	**93.3** 55.1 (10.3)	**81.8** 141.2 (21.3)	**100.0** 23.0 (19.5)	**70.0** 9.4 (3.4)	**100.0** 28.4 (8.9)	**100.0** 45.6 (7.8)	**100.0** 51.1 (5.9)	**73.3** 90.2 (26.6)	**20.0** 1.4 (1.4)	**68.2** 11.8 (4.2)	**86.7** 47.2 (7.8)	**73.3** 38.1 (9.8)	**71.9** 62.6 (20.4)
Crepidostomum pseudofarionis, C. farionis & *C. metoecus*[b]	*	**86.7** 8.7 (2.0)	**93.3** 8.5 (2.2)	**87.1** 9.8 (2.3)	**80.0** 20.6 (6.7)	**27.3** 1.3 (0.6)	-	**90.0** 8.0 (2.9)	**95.5** 11.5 (5.3)	**75.8** 2.8 (0.6)	**60.6** 5.6 (2.7)	**16.7** 1.2 (0.6)	**100.0** 9.2 (5.1)	**77.3** 14.5 (6.8)	**93.3** 13.9 (6.3)	**70.0** 3.0 (1.0)	**68.8** 10.1 (3.6)
Cestoda																	
Dibothriocephalus dendriticus & *D. ditremus*[b]	**	**100.0** 41.7 (5.1)	**100.0** 39.1 (6.7)	**100.0** 35.8 (6.4)	**100.0** 16.0 (3.0)	**90.9** 26.7 (12.3)	-	**50.0** 0.8 (0.3)	**86.4** 16.2 (12.0)	**97.0** 10.7 (6.4)	**90.9** 25.0 (9.9)	**93.3** 49.3 (15.1)	-	**4.6** 0.05 (0.05)	**56.7** 27.8 (10.5)	**80.0** 96.0 (28:6)	**78.1** 178.4 (68.1)
Eubothrium salvelini	*	**20.0** 0.5 (0.2)	**53.3** 1.1 (0.2)	**90.3** 2.1 (0.4)	**26.7** 0.3 (0.1)	**66.7** 4.6 (1.3)	-	**20.0** 0.3 (0.2)	**27.3** 1.0 (0.4)	**78.8** 3.3 (0.7)	**66.7** 1.9 (0.4)	**70.0** 2.1 (0.4)	-	-	**3.3** 0.03 (0.03)	-	**34.4** 1.3 (0.5)
Proteocephalus sp.	*	**3.3** 0.03 (0.03)	**16.7** 0.5 (0.4)	**22.6** 0.4 (0.1)	**46.7** 3.9 (2.1)	**6.1** 0.1 (0.1)	-	**10.0** 0.1 (0.1)	-	**3.0** 0.03 (0.03)	**3.0** 0.1 (0.1)	-	-	-	-	-	**6.3** 0.1 (0.04)
Nematoda																	
Contracaecum sp.	**	**3.3** 0.03 (0.03)	-	-	-	**9.1** 0.2 (0.1)	-	-	-	-	-	**13.3** 0.2 (0.1)	-	-	-	-	-
Pseudocapillaria (Ichthyocapillaria) salvelini	*	-	-	**3.2** 0.03 (0.03)	-	**27.3** 11.9 (5.3)	-	**10.0** 0.1 (0.1)	**9.1** 0.2 (0.1)	**3.0** 0.03 (0.03)	-	**80.0** 40.2 (11.6)	-	**86.4** 9.6 (2.8)	-	-	**6.3** 0.1 (0.1)
Philonema oncorhynchi	*	-	-	-	-	**15.2** 0.3 (0.1)	-	-	-	-	-	40.0 0.8 (0.3)	-	**4.6** 0.05 (0.05)	-	-	**3.1** 0.03 (0.03)
Salmonema ephemeridarum	*	-	**3.3** 0.03 (0.03)	-	-	-	-	-	**27.3** 1.3 (1.0)	**24.2** 1.0 (0.6)	**9.1** 0.1 (0.1)	-	**40.0** 0.8 (0.6)	-	**80.0** 10.6 (3.2)	**33.3** 4.0 (1.9)	**18.8** 3.9 (2.5)
Copepoda																	

Salminicola edwardsii	*	**30.0** 0.3 (0.1)	**13.3** 0.2 (0.1)	**12.9** 0.2 (0.1)	**13.3** 0.2 (0.1)	**9.1** 0.1 (0.1)	-	-	-	-	**3.0** 0.03 (0.03)	**23.3** 0.6 (0.2)	-	-	-	-	-
Species richness (*S*)		**9**	**9**	**10**	**8**	**13**	**2**	**8**	**8**	**10**	**10**	**11**	**5**	**7**	**7**	**6**	**11**

[a]Prevalence and abundance estimated from a single eye.

[b]The taxa distinguishable only using microscopic techniques or molecular data were analysed together.

Figures

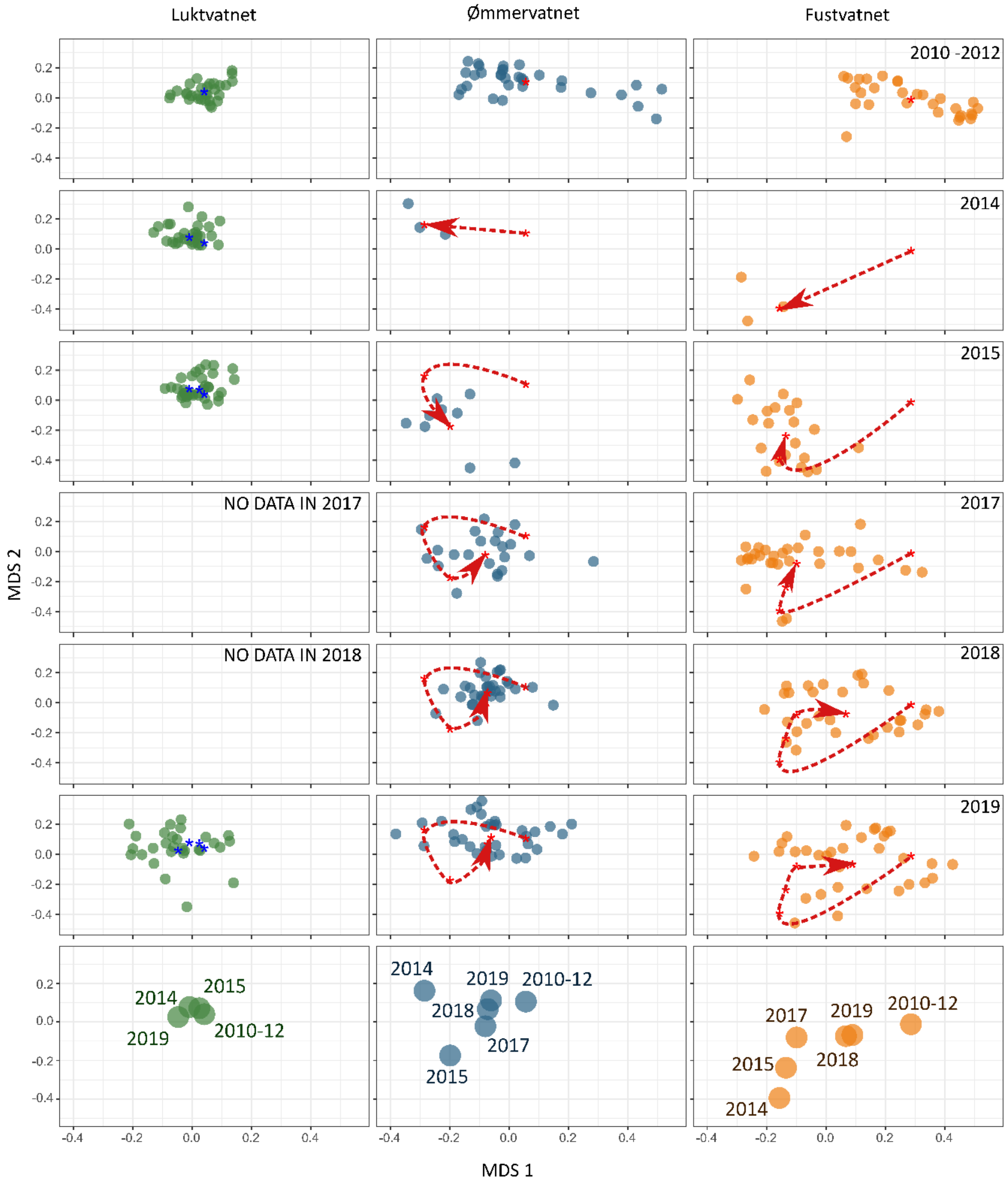

Figure 1: Multidimensional scaling biplot based on Bray–Curtis dissimilarity among parasite infracommunities through time (N=398). Infracommunities are colour-coded according to the lake (green, Luktvatnet, control; blue,

Ømmervatnet, treated; orange, Fustvatnet, treated). The position of the asterisks indicates the mean of the parasite infracommunities for each year and the arrows indicate the change of mean over the years.

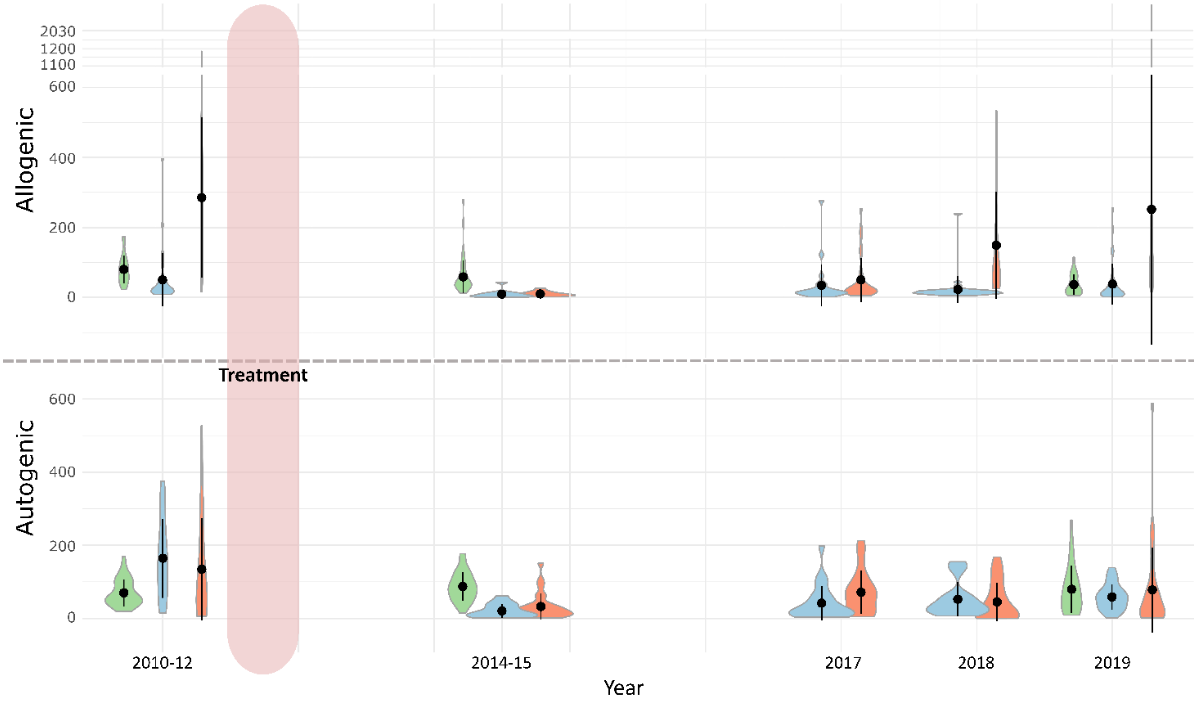

Figure 2: Mean abundances of allogenic and autogenic parasites individuals over time in the two treated lakes (Fustvatnet in orange and Ømmervatnet in blue) and the untreated lake (Luktvatnet in green). Note the break in the y axis.

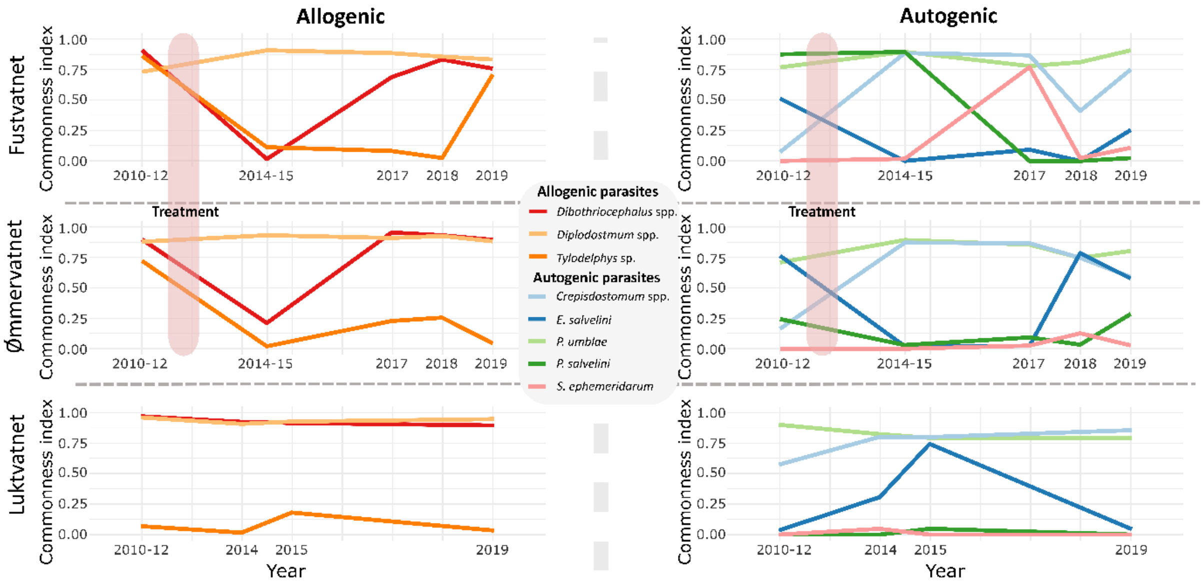

Figure 3: Illustrates the variation in commonness indices for both common and rare species from the periods 2010-12 to 2019. It visualizes the degree of variation in these indices over time, providing insights into shifts in species prevalence and rarity across the studied interval. Data for both allogenic and autogenic parasite taxa are presented. This graphical representation facilitates an understanding of temporal dynamics within the species community.

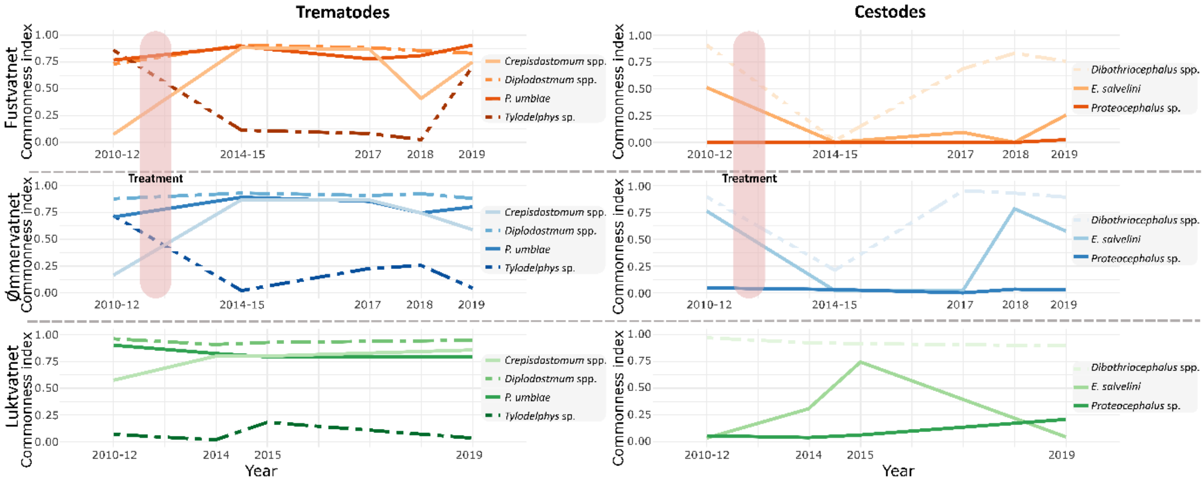

Figure 4: Illustrates the variation in commonness indices for common and rare species between the periods 2010-12 and 2019, separated by lake. Data for both trematodes and cestodes are presented. Dashed lines represent allogenic species, while solid lines indicate autogenic species. This visualization helps in understanding the temporal shifts in species commonality and rarity, differentiated by parasite type and species origin across the studied lakes.

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Conflict of interest

None declared.

Data accessibility

The DNA sequences will be submitted to Genbank upon manuscript submission (https://www.ncbi.nlm.nih.gov/genbank/).

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Supplementary tables

Supplementary Table S1: Species sequenced in the study along with their corresponding host localities: Fustvatnet (FU), Ømmervatnet (ØM), and Luktvatnet (LU). It also provides the GenBank accession numbers for each sequence, facilitating further research and verification of the genetic data obtained from these species.

Species	Location	Gene	GenBank acc. nos.
TREMATODA			
Apatemon gacilis	ØM	28S	XXX - XXX
Crepidostomum farionis	FU and LU	28S	XXX - XXX
Crepidostomum pseudofarionis	FU	28S	XXX - XXX
Diplostomum sp.	FU and LU	28S	XXX - XXX
Phyllodistomum umblae	FU, ØM and LU	28S	XXX - XXX
CESTODA			
Dibothriocephalus spp.	FU, ØM and LU	28S	XXX - XXX
Eubothrium salvelini	FU, ØM and LU	28S	XXX - XXX
Proteocephalus sp.	FU, ØM and LU	28S	XXX - XXX
NEMATODA			
Philonema oncorhynchi	FU and ØM	18S	XXX - XXX
Salmonema ephemeridarum	FU and ØM	18S	XXX - XXX

Supplementary Table S2: Summarizes the results from a PERMANOVA test performed using the vegan::adonis2 function to assess differences in the full parasite infracommunity. It details the source of variation, sum of squares, degrees of freedom, mean squares, F-statistic values, and associated p-values, providing insights into the community structure variations across the groups studied.

	Df	Sum of squares	R2	F-values	P-values
Locality	2	4.98	0.14	45.39	**0.001**
Year	5	5.22	0.14	19.02	**0.001**
Locality*Year	8	5.72	0.16	13.05	**0.001**
Residual	382	20.94	0.57		
Total	397	36.86	1.00		

Supplementary Table S3: Chi-square analysis on the Luktvanet parasite prevalences. The results of a chi-square analysis assessing the prevalence of parasites in Luktvanet. It includes, expected frequencies, chi-square values, degrees of freedom, and p-values for each tested variable.

	Chi-square residual

	2010-12	2014	2015	2019
Diplostomum sp.	0.502	0.158	-1.076	0.502
Tylodelphys sp.	1.841	-2.350	1.933	-1.542
Apatemon gracilis.	-0.876	-0.891	2.457	-0.876
Phyllodistomum umblae	0.670	0.326	-0.907	-0.020
Crepidostomum pseudofarionis, C. farionis & C. metoecus	0.455	0.857	-0.969	-0.278
Dibothriocephalus spp.	0.502	0.158	-1.076	0.502
Eubrothrium salvelini	-3.754	0.949	**5.130**	-2.763
Proteocephalus sp.	-3.883	-1.130	-0.454	**5.524**
Contracaecum sp.	2.854	-0.906	-0.963	-0.890
Pseudocapillaria (Ichthyocapillaria) salvelini	-0.876	-0.891	2.457	-0.876
Salmonema ephemeridarum	-0.890	2.775	-0.963	-0.890
Salminicola edwardsii	3.309	-0.915	-1.469	-0.789

X-squared = 169.95, df = 33, p-value < 2.2e-16 ***

Supplementary Table S4: Summarizes the results from a PERMANOVA test performed using the vegan::adonis2 function to assess differences in Luktvatnet full parasite infracommunity. It details the source of variation, sum of squares, degrees of freedom, mean squares, F-statistic values, and associated p-values, providing insights into the community structure variations across the groups studied.

	Df	Sum of squares	R2	F-values	P-values
Year	3	0.48	0.14	7.00	**0.001**
Length	1	0.22	0.06	9.75	**0.001**
Age	1	0.02	0.01	1.01	0.379
Residual weight	1	0.06	0.02	2.47	**0.037**
Year*Age	3	0.18	0.05	2.59	**0.003**
Residual	109	2.50	0.72		
Total	118	3.46	1.00		

Supplementary Table S5: Results of a PERMANOVA test conducted on the Luktvanet parasite infracommunity across different years, utilizing the pairwiseadonis2::pairwiseadonis2 function. The table includes F-values, displayed in white in the top right of each cell, and corresponding p-values, shown in grey in the bottom left.

LU10-12	LU14	LU15	LU19

LU10-12		-26.56	-28.94	-20.06
LU14	0.789		567.71	-5.59
LU15	0.818	0.309		-27.99
LU19	0.723	0.815	0.732	

Supplementary Table S6: Results of a Joint Species Distribution Model (JSDM) analysis conducted on the parasite infracommunity within Luktvatnet, designated as the control lake. It details the model coefficients, standard errors, z-values, and p-values, offering insights into the associations and interactions between different parasite species within the lake's ecosystem.

	Wald-value	P-value
Intercept	19.299	**0.001**
2010-12 VS 2014	9.08	0.299
2010-12 VS 2015	10.401	0.169
2010-12 VS 2019	9.775	0.207
Host length	11.139	0.116
Host residual weight	5.518	0.758
Host length : 2010-12 VS 2014	9.249	0.29
Host length : 2010-12 VS 2015	10.813	0.136
Host length : 2010-12 VS 2019	8.858	0.313
Host residual weight : 2010-12 VS 2014	5.221	0.788
Host residual weight : 2010-12 VS 2015	7.169	0.759
Host residual weight : 2010-12 VS 2019	8.42	0.313

Supplementary Table S7: Results from a Generalized Linear Model (GLM) analysis evaluating changes in autogenic and allogenic abundances over time in Luktvatnet, the control lake. It includes coefficients, standard errors, z-values, and p-values, detailing the temporal dynamics of these parasite groups. The analysis helps to understand the population trends and environmental impacts on autogenic and allogenic species in the lake ecosystem.

Variable level	Estimate	SE	*t* value	*P*
Intercept (Allogenic and 2010-12)	-41.97	35.75	-1.17	0.2417
Autogenic	1.55	50.56	0.03	0.9755
2014	-14.93	11.23	-1.33	0.1850
2015	-11.69	11.13	-1.05	0.2945
2019	-17.60	15.14	-1.16	0.2463
Host length	0.50	0.14	3.55	**4.73e-4**
Host residual weight	18.91	45.96	0.41	0.6811
Autogenic : 2014	38.66	15.88	2.44	**0.0157**
Autogenic : 2015	37.53	15.73	2.39	**0.0179**
Autogenic : 2019	53.32	21.42	2.49	**0.0135**
Autogenic : Host length	-0.05	0.20	-0.26	0.7978
Autogenic : Host residual weight	18.66	65.00	0.29	0.7743
Intercept (Autogenic and 2019)	-4.70	27.51	-0.17	0.8645

Allogenic	-54.87	38.90	-1.41	0.1598
2010-12	-35.71	15.14	-2.36	**0.0192**
2014	-11.98	13.80	-0.87	0.3865
2015	-9.87	13.70	-0.72	0.4721
Host length	0.45	0.14	3.19	**1.65e-3**
Host residual weight	37.57	45.96	0.82	0.4145
Allogenic : 2010-12	53.32	21.42	2.49	**0.0135**
Allogenic : 2014	14.65	19.52	0.75	0.4536
Allogenic : 2015	15.78	19.38	0.82	0.4163
Allogenic : Host length	0.05	0.20	0.26	0.7978
Allogenic : Host residual weight	-18.66	65.00	-0.29	0.7743

Supplementary Table S8: Results from a Generalized Linear Model (GLM) analysis evaluating changes in autogenic and allogenic abundances over time in Fustvatnet, the control lake. It includes coefficients, standard errors, z-values, and p-values, detailing the temporal dynamics of these parasite groups. The analysis helps to understand the population trends and environmental impacts on autogenic and allogenic species in the lake ecosystem.

Variable level	Estimate	SE	t-value	*P*-value
Intercept (Allogenic and 2010-12)	12.04	93.40	0.13	0.8975
Autogenic	112.23	132.09	0.85	0.3963
2014-15	-229.56	47.50	-4.83	**2.22E-06**
2017	-222.12	43.74	-5.08	**6.98E-07**
2018	-116.12	44.10	-2.63	**8.93E-03**
2019	-33.06	44.10	-0.75	0.4541
Host length	1.03	0.33	3.10	**2.15E-03**
Host residual weight	14.23	178.71	0.08	0.9366
Autogenic : 2014-15	128.87	67.17	1.92	0.0561
Autogenic : 2017	159.86	61.86	2.58	**0.0103**
Autogenic : 2018	25.61	62.37	0.41	0.6817
Autogenic : 2019	-18.33	62.36	-0.29	0.7690
Autogenic : Host length	-0.99	0.47	-2.11	**0.0355**
Autogenic : Host residual weight	81.98	252.74	0.32	0.7459
Intercept (Allogenic and 2019)	-21.02	93.88	-0.22	0.8230
Autogenic	93.90	132.76	0.71	0.4800
2010-12	33.06	44.10	0.75	0.4541
2014-15	-196.50	47.83	-4.11	**5.23E-05**
2017	-189.06	43.69	-4.33	**2.10E-05**
2018	-83.07	44.95	-1.85	0.0656
Autogenic : 2010-12	43.94	63.57	0.69	0.4900
Autogenic : 2014-15	18.33	62.36	0.29	0.7690

Autogenic : 2017	147.20	67.64	2.18	**0.0304**
Autogenic : 2018	178.19	61.79	2.88	**4.23E-03**
Intercept (Allogenic and 2018)	-104.08	87.02	-1.20	0.2327
Autogenic	137.84	123.06	1.12	0.2637
2010-12	116.12	44.10	2.63	**8.93E-03**
2014-15	-113.43	45.58	-2.49	**0.0134**
2017	-105.99	43.39	-2.44	**0.0152**
2019	83.07	44.95	1.85	0.0656
Autogenic : 2010-12	-25.61	62.37	-0.41	0.6817
Autogenic : 2014-15	103.26	64.46	1.60	0.1103
Autogenic : 2017	134.25	61.37	2.19	**0.0295**
Autogenic : 2019	-43.94	63.57	-0.69	0.4900
Intercept (Allogenic and 2017)	-210.08	89.34	-2.35	**0.0194**
Autogenic	272.09	126.34	2.15	**0.0321**
2010-12	222.12	43.74	5.08	**6.98E-07**
2014-15	-7.44	46.05	-0.16	0.8717
2018	105.99	43.39	2.44	**0.0152**
2019	189.06	43.69	4.33	**2.10E-05**
Autogenic : 2010-12	-134.25	61.37	-2.19	**0.0295**
Autogenic : 2014-15	-178.19	61.79	-2.88	**4.23E-03**
Autogenic : 2018	-159.86	61.86	-2.58	**0.0103**
Autogenic : 2019	-30.99	65.12	-0.48	0.6345
Intercept (Allogenic and 2014-15)	-217.52	80.33	-2.71	**7.19E-03**
Autogenic	241.09	113.61	2.12	**0.0347**
2010-12	229.56	47.50	4.83	**2.22E-06**
2017	7.44	46.05	0.16	0.8717
2018	113.43	45.58	2.49	**0.0134**
2019	196.50	47.83	4.11	**5.23E-05**
Autogenic : 2010-12	30.99	65.12	0.48	0.6345
Autogenic : 2017	-103.26	64.46	-1.60	0.1103
Autogenic : 2018	-147.20	67.64	-2.18	**0.0304**
Autogenic : 2019	-128.87	67.17	-1.92	0.0561
Intercept (Autogenic and 2010-12)	124.27	93.40	1.33	0.1845
Allogenic	-112.23	132.09	-0.85	0.3963
2014-15	-100.69	47.49	-2.12	**0.0349**
2017	-62.26	43.74	-1.42	0.1558
2018	-90.52	44.10	-2.05	**0.0411**
2019	-51.39	44.10	-1.17	0.2449
Host length	0.04	0.33	0.11	0.9124
Host residual weight	96.21	178.71	0.54	0.5908
Allogenic : 2014-15	-128.87	67.17	-1.92	0.0561
Allogenic : 2017	-159.86	61.86	-2.58	**0.0103**

Allogenic : 2018	-25.61	62.37	-0.41	0.6817
Allogenic : 2019	18.33	62.36	0.29	0.7690
Allogenic : Host length	0.99	0.47	2.11	**0.0355**
Allogenic : Host residual weight	-81.98	252.74	-0.32	0.7459
Intercept (Autogenic and 2019)	72.88	93.88	0.78	0.4382
Allogenic	-93.90	132.76	-0.71	0.4800
2010-12	51.39	44.10	1.17	0.2449
2014-15	-49.30	47.83	-1.03	0.3035
2017	-10.87	43.69	-0.25	0.8037
2018	-39.13	44.95	-0.87	0.3847
Allogenic : 2010-12	-18.33	62.36	-0.29	0.7690
Allogenic : 2014-15	-147.20	67.64	-2.18	**0.0304**
Allogenic : 2017	-178.19	61.79	-2.88	**4.23E-03**
Allogenic : 2018	-43.94	63.57	-0.69	0.4900

Supplementary Table S9: Results from a Generalized Linear Model (GLM) analysis evaluating changes in autogenic and allogenic abundances over time in Ømmervatnet, the control lake. It includes coefficients, standard errors, z-values, and p-values, detailing the temporal dynamics of these parasite groups. The analysis helps to understand the population trends and environmental impacts on autogenic and allogenic species in the lake ecosystem.

Variable level	Estimate	SE	t-value	*P*-value
Intercept (Autogenic and 2010-12)	200.19	34.10	5.87	**1.37E-08**
Allogenic	-239.34	48.22	-4.96	**1.28E-06**
2014-15	-153.42	22.28	-6.89	**4.64E-11**
2017	-121.27	17.50	-6.93	**3.60E-11**
2018	-108.00	15.55	-6.95	**3.21E-11**
2019	-105.72	15.13	-6.99	**2.53E-11**
Host length	-0.14	0.14	-1.02	0.3072
Host residual weight	82.43	60.01	1.37	0.1708
Allogenic : 2014-15	117.05	31.51	3.72	**2.51E-04**
Allogenic : 2017	96.00	24.75	3.88	**1.35E-04**
Allogenic : 2018	69.38	21.98	3.16	**1.80E-03**
Allogenic : 2019	89.86	21.40	4.20	**3.72E-05**
Allogenic : Host length	0.51	0.20	2.62	**9.24E-03**
Allogenic : Host residual weight	-158.08	84.87	-1.86	0.0637
Intercept (Autogenic and 2019)	94.46	36.22	2.61	**9.65E-03**
Allogenic	-149.48	51.22	-2.92	**3.84E-03**
2010-12	105.72	15.13	6.99	**2.53E-11**
2014-15	-47.69	21.43	-2.23	**0.0269**
2017	-15.55	16.71	-0.93	0.3530
2018	-2.27	14.95	-0.15	0.8792
Allogenic : 2010-12	-89.86	21.40	-4.20	**3.72E-05**

Allogenic : 2014-15	27.19	30.30	0.90	0.3705
Allogenic : 2017	6.14	23.63	0.26	0.7954
Allogenic : 2018	-20.49	21.14	-0.97	0.3333
Intercept (Autogenic and 2018)	92.19	38.37	2.40	**0.0170**
Allogenic	-169.97	54.26	-3.13	**1.94E-03**
2010-12	108.00	15.55	6.95	**3.21E-11**
2014-15	-45.42	21.91	-2.07	**0.0392**
Allogenic : 2017	-13.28	16.62	-0.80	0.4251
Allogenic : 2019	2.27	14.95	0.15	0.8792
Allogenic : 2010-12	-69.38	21.98	-3.16	**1.80E-03**
Allogenic : 2014-15	47.68	30.98	1.54	0.1251
Allogenic : 2019	26.62	23.50	1.13	0.2583
LCAllogenic:Year_pool2019	20.49	21.14	0.97	0.3333
Intercept (Autogenic and 2017)	78.91	39.41	2.00	**0.0463**
Allogenic	-143.34	55.73	-2.57	**0.0107**
2010-12	121.27	17.50	6.93	**3.60E-11**
2014-15	-32.14	22.48	-1.43	0.1541
2018	13.28	16.62	0.80	0.4251
2019	15.55	16.71	0.93	0.3530
Allogenic : 2010-12	-96.00	24.75	-3.88	**1.35E-04**
Allogenic : 2014-15	21.05	31.80	0.66	0.5085
Allogenic : 2018	-26.62	23.50	-1.13	0.2583
Allogenic : 2019	-6.14	23.63	-0.26	0.7954
Intercept (Autogenic and 2014-15)	46.77	39.60	1.18	0.2387
Allogenic	-122.29	56.00	-2.18	**0.0299**
2010-12	153.42	22.28	6.89	**4.64E-11**
2017	32.14	22.48	1.43	0.1541
2018	45.42	21.91	2.07	**0.0392**
2019	47.69	21.43	2.23	**0.0269**
Allogenic : 2010-12	-117.05	31.51	-3.72	**2.51E-04**
Allogenic : 2017	-21.05	31.80	-0.66	0.5085
Allogenic : 2018	-47.68	30.98	-1.54	0.1251
Allogenic : 2019	-27.19	30.30	-0.90	0.3705
Intercept (Allogenic and 2010-12)	-39.16	34.10	-1.15	0.2519
Autogenic	239.34	48.22	4.96	**1.28E-06**
2014-15	-36.36	22.28	-1.63	0.1040
2017	-25.28	17.50	-1.44	0.1500
2018	-38.62	15.55	-2.49	**0.0136**
2019	-15.86	15.13	-1.05	0.2955
Host length	0.37	0.14	2.69	**0.0077**
Host residual weight	-75.65	60.01	-1.26	0.2087
Autogenic : 2014-15	-117.05	31.51	-3.72	**0.0003**

Autogenic : 2017	-96.00	24.75	-3.88	**0.0001**
Autogenic : 2018	-69.38	21.98	-3.16	**0.0018**
Autogenic : 2019	-89.86	21.40	-4.20	**3.72E-05**
Autogenic : Host length	-0.51	0.20	-2.62	**0.0092**
Autogenic : Host residual weight	158.08	84.87	1.86	**0.0637**
Intercept (Allogenic and 2019)	-55.02	36.22	-1.52	0.1300
Autogenic	149.48	51.22	2.92	**0.0038**
2010-12	15.86	15.13	1.05	0.2955
2014-15	-20.50	21.43	-0.96	0.3396
2017	-9.41	16.71	-0.56	0.5737
2018	-22.76	14.95	-1.52	0.1290
Autogenic : 2010-12	89.86	21.40	4.20	**3.72E-05**
Autogenic : 2014-15	-27.19	30.30	-0.90	0.3705
Autogenic : 2017	-6.14	23.63	-0.26	0.7954
Autogenic : 2018	20.49	21.14	0.97	0.3333

Supplementary Table S10: Summarizes the results from a PERMANOVA test performed using the vegan::adonis2 function to assess differences in Ømmervatnet parasite infracommunity. It details the source of variation, sum of squares, degrees of freedom, mean squares, F-statistic values, and associated p-values, providing insights into the community structure variations across the groups studied.

	Df	Sum of squares	R2	F-values	P-values
Year	4	2.00	0.19	8.48	**0.001**
Host length	1	0.72	0.07	12.28	**0.001**
Host residual weight	1	0.25	0.02	4.21	**0.001**
Year : Host length	4	0.60	0.06	2.54	**0.002**
Residual	121	7.14	0.67		
Total	131	10.71	1.00		

Supplementary Table S11: Summarizes the results from a PERMANOVA test performed using the vegan::adonis2 function to assess differences in Fustvatnet parasite infracommunity. It details the source of variation, sum of squares, degrees of freedom, mean squares, F-statistic values, and associated p-values, providing insights into the community structure variations across the groups studied.

	Df	Sum of squares	R2	F-values	**P-values**
Year	4	7.36	0.41	26.16	**0.001**
Host length	1	0.25	0.01	3.55	**0.013**
Host residual weight	1	0.27	0.01	3.80	**0.006**
Year : Host length	4	0.45	0.02	1.58	**0.079**
Residual	136	9.57	0.53		
Total	146	17.89	1.00		

Supplementary Table S12: Results of a PERMANOVA test conducted on the Fustvatnet parasite infracommunity across different years, utilizing the pairwiseadonis2::pairwiseadonis2 function. The table includes F-values, displayed in white in the top right of each cell, and corresponding p-values, shown in grey in the bottom left.

	FU10-12	FU14-15	FU17	FU18	FU19
FU10-12		1.43E+11	-23.18	86.93	-28.45
FU14-15	**0.001*****		-24.84	0.51	31.83
FU17	0.931	0.947		244.39	-28.69
FU18	0.156	0.508	0.297		-23.82
FU19	0.718	0.36	0.787	0.63	

Supplementary Table S13: Results of a PERMANOVA test conducted on the Ømmervatnet parasite infracommunity across different years, utilizing the pairwiseadonis2::pairwiseadonis2 function. The table includes F-values, displayed in white in the top right of each cell, and corresponding p-values, shown in grey in the bottom left.

	ØM10-12	ØM14-15	ØM17	ØM18	ØM19
ØM10-12		4.73	-13.1	1795.4	48.95
ØM14-15	0.519		227.55	118.04	-10.4
ØM17	0.797	0.184		723.01	-17.06
ØM18	0.392	**0.027 ***	**0.044 ***		-28.88
ØM19	0.238	0.484	0.519	0.634	

Supplementary Table S14: Results of a Joint Species Distribution Model (JSDM) analysis conducted on the parasite infracommunity within Fustvatnet, designated as the control lake. It details the model coefficients, standard errors, z-values, and p-values, offering insights into the associations and interactions between different parasite species within the lake's ecosystem.

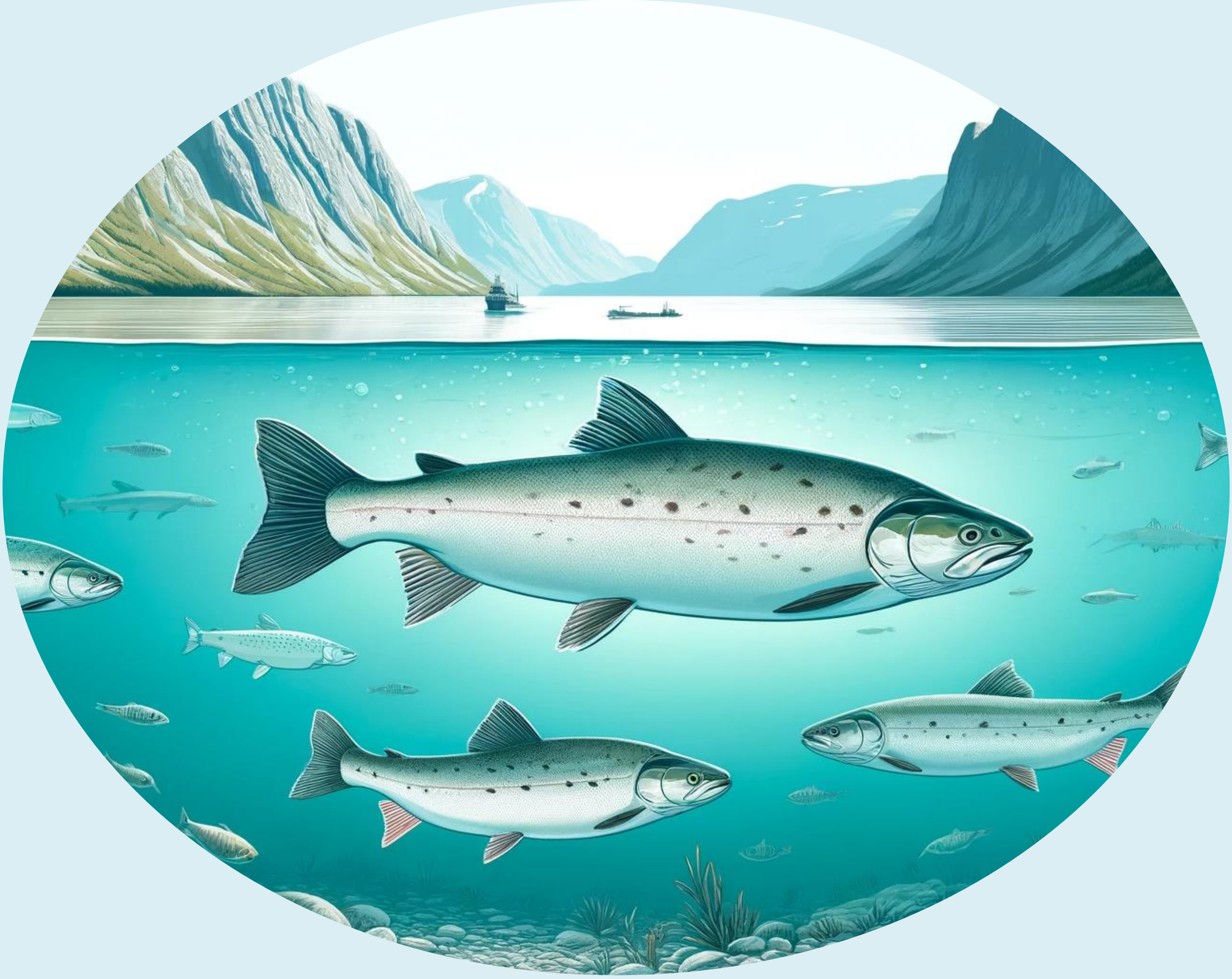
	Wald-value	P-value
(Intercept)	102.61	**0.001**
2010-12 VS 2014-15	11.99	0.355
2010-12 VS 2017	24.65	0.09
2010-12 VS 2018	21.70	0.168
2010-12 VS 2018	49.51	**0.002**
Host length	30.83	**0.021**
Host residual weight	20.86	0.191
Host length : 2010-12 VS 2014-15	6.22	0.861
Host length : 2010-12 VS 2017	21.79	0.157
Host length : 2010-12 VS 2018	22.46	0.144
Host length : 2010-12 VS 2019	51.28	**0.002**
Host residual weight : 2010-12 VS 2014-15	13.42	0.163
Host residual weight : 2010-12 VS 2017	9.45	0.757
Host residual weight : 2010-12 VS 2018	3.94	0.986

Host residual weight : 2010-12 VS 2019	13.88	0.505

Supplementary Table S15: Results of a Joint Species Distribution Model (JSDM) analysis conducted on the parasite infracommunity within Ømmervatnet, designated as the control lake. It details the model coefficients, standard errors, z-values, and p-values, offering insights into the associations and interactions between different parasite species within the lake's ecosystem.

	Wald-value	P-value
(Intercept)	32.96	**0.001**
2010-12 VS 2014-15	6.15	0.641
2010-12 VS 2017	17.02	**0.037**
2010-12 VS 2018	15.47	0.097
2010-12 VS 2018	12.46	0.224
Host length	26.87	**0.005**
Host residual weight	19.47	**0.049**
Host length : 2010-12 VS 2014-15	11.04	0.095
Host length : 2010-12 VS 2017	20.04	**0.006**
Host length : 2010-12 VS 2018	17.54	**0.036**
Host length : 2010-12 VS 2019	15.38	0.095
Host residual weight : 2010-12 VS 2014-15	4.87	0.769
Host residual weight : 2010-12 VS 2017	13.78	0.114
Host residual weight : 2010-12 VS 2018	19.09	**0.013**
Host residual weight : 2010-12 VS 2019	19.25	**0.026**

Paper III



Assessing parasite communities in anadromous Arctic charr: is it a cost of migration?

Authors

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Keywords

Diadromous, salmonids, parasite infracommunities, helminths, freshwater, marine.

Abstract

This study investigates the potential parasitic infection costs associated with anadromous migration in Arctic charr (Salvelinus alpinus L.) by analysing their parasite community structure from the freshwater and marine environment across two consecutive years. Our research specifically focuses on how seasonal migration from fresh- to marine-waters and marine feeding behaviour affect the parasite load of the first- and second-year migrants. As hypothesized, marine-migratory Arctic charr exhibited more species-rich and abundant parasite communities compared to pre- and post-migrants caught in freshwater. Additionally, the marine parasite community composition remains consistent over two successive years among the migrants. Our findings confirmed that migratory Arctic charr notably had high infection rate of trophically transmitted marine parasites, resulting from increased exposure during their short marine feeding migration. Our results highlight the balance between the parasitic burden and

the benefits of a forging migration, such as enhanced growth. Importantly, ascendent migration acts as an escape mechanism from many marine parasites, as most are being lost after returning to freshwater. The potential culling effect of parasitism on the migrants, combined with natural selection could be favouring more resistant individuals, potentially improving the population resilience. This research aims to highlights the ecological and evolutionary implications of a potential cost of parasitism in migratory species. This study also highlights the importance of ongoing monitoring and further research studies to understand and address the impacts of anthropogenic induced environmental changes on migratory fish populations.

Introduction

Migration behaviour is observed across various taxonomic groups (Chapman *et al*., 2014), whereby animals exhibit seasonal movement from one location to another, often covering vast distances (Mueller & Fagan, 2008; Dingle, 2014). The benefit of animal migration are diverse, such as the exploitation of seasonal resource abundance, avoidance of harsh environmental conditions, and optimizing reproductive success (see Alerstam *et al*., 2003; Shaw, 2016). However, this adaptive strategy may come at a considerable cost, requiring significant energy expenditure (Dingle, 2014), altered exposure to predation and infection risks (Altizer *et al*., 2011), and potential challenges in navigating unfamiliar territories (see Bonte *et al*., 2012). Additionally, migratory behaviour varies within species and populations, with some individuals migrating, whereas others do not (Shaw, 2016). One of the important components of migration is feeding migration, where animals undertake extensive journeys in search of optimal foraging areas (e.g. in birds Lack, 1968; and in whales Lockyer & Brown, 1981). The quest for abundant food resources drives species to cross ecosystems, shaping intricate patterns of movement that profoundly influence ecological dynamics.

Diadromous characterizes a fish migration between two habitats (Gross, 1987; McDowall, 1997). Among these, the anadromous migration describes the migration from freshwater to marine environments for foraging and back to freshwater for breeding (Grainger, 1953; Gross *et al*., 1988; McDowall, 1997). One of the well-studied groups of anadromous fishes are the salmonids, such as e.g. Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.), and Arctic charr (*Salvelinus alpinus* L.). The benefits of anadromy are “easy” to observe. For example, the Atlantic salmon grows from a smolt of 30 to 50 g at the start of their migration to reach an adult side of 1 to 3 kg after one years at sea (Barson *et al*., 2015; Ytrestøyl & Mathisen, 2023). In contrast, the migration costs of anadromy can be harder to quantify (e.g. altered predation risk, and parasite infections; Altizer *et al*., 2011; Jensen *et al*., 2018). The cost associated with anadromy is high as the first-time migrants (smolts) may be subjected to mortality rates as high as 70% (brown trout) to 90% (Atlantic salmon) in the marine system (e.g. Hansen & Quinn, 1998; Jensen *et al*., 2019). Mortality during marine migrations can result from a number of stressors, such as the physiological costs of adaptations to cope with osmoregulatory transitions (Hoar, 1976; Finstad *et al*., 1989) that stress can decrease the survival to maturity (Hendry *et al*., 2004). Moreover, the transition to the marine environment exposes fish to more predators, like marine mammals, larger fish, and seabirds (e.g. Krkošek *et al*., 2007; Thorstad *et al*., 2016), than in the freshwater habitat. For instance, sea lice (e.g. *Lepeophtheirus salmonis salmonis*) are known for their negative impact on the survival of migratory salmonids in the wild (Thorstad *et al*., 2015; Forseth *et al*., 2017). Marine endoparasitic tapeworms (e.g. *Eubothrium* spp.) are found to have sublethal effects by reducing the growth of Atlantic salmon in farms (Bristow & Berland, 1991). However, we lack information about the full extent of endoparasite burdens on wild salmonid health during residency in the marine environment (Holst *et al*., 1993; Bristow *et al*., 1996; Knudsen *et al*., 2005).

Anadromous Arctic charr is the most cold-water adapted salmonid species globally (Johnson, 1980; Klemetsen *et al*., 2003), and displays remarkable plasticity in its life history strategies (Adams, 1998), with some populations adopting facultative anadromy while others remain resident in freshwater (Nordeng, 1983; Tallman *et al*., 1996; Klemetsen *et al*., 2003). Anadromous individuals typically spend ~30 to 60 days in the marine environment (Berg & Berg, 1993; Jensen *et al*., 2020) during which time they double in weight from ~213 to 499 g (Young *et al*., 2021; Nilsen Opheim, 2022; Grenier *et al*., Unpublished). Similar to other salmonid species, the costs for the smolts/first time migrants are high with 70% mortality (Rikardsen *et al*., 1997; Jensen *et al*., 2019). This high mortality is primarily attributed to predation (Scharf *et al*., 2000), osmoregulatory stress (Jensen *et al*., 2012), and ectoparasitic infections (Fjelldal *et al*., 2019). Little is known about the mortality (direct or indirect) effects from the endoparasite community of wild anadromous Arctic charr. Indeed, previous studies, only carried out in North America, focused on describing anadromous Arctic charr parasite community and their use as indicators of marine migration (Bouillon & Dempson, 1989; Due & Curtis, 1995; McDonald & Margolis, 1995; Isinguzo, 2009) without assessing the infection burdens. McDonald and Margolis (1995) reported that anadromous Arctic charr from North America are infected by a variety of generalist parasites (~28 marine species) shared with marine fish (e.g. cod & herring), which reflect its host feeding behaviour (Knudsen *et al*., 2003;

Grenier *et al*., Unpublished). Thus, no studies of anadromous Arctic charr parasite community structure are so far done in Europe.

Our study aims to highlight the potential parasitic infection cost of anadromy for Arctic charr through mapping their parasite community structure in the freshwater phase and the marine environment. We seek to link the seasonal migration of the Arctic charr in two successive years with their feeding in the marine environment and how this influences the parasite community. We expect the most inexperienced anadromous Arctic charr (i.e. first- and second-year migrants) to be predominantly infected by trophically transmitted marine parasites due to their extensive feeding in the marine environment.

We first hypothesize that the parasite community of migratory Arctic charr will be more species-rich than non-migrating parr. Secondly, we hypothesize that migratory Arctic charr will exhibit a higher abundance of trophically transmitted parasites compared to the parasite community observed in non-migrating freshwater parr. Thirdly, we hypothesize that the marine parasite community composition will be similar among the marine migrants over two successive years after returning from the sea.

Material and Methods

Sampling site

Our study takes place in Laksvatn (69°38′ N, 19°38′ E) - Balsfjord lake-fjord system in northern Norway. The lake is characterized by its relatively shallow nature, boasting an average depth of 6 m, a maximum depth of 15 m and a surface area of 0.8 km^2. While predominantly inhabited by anadromous Arctic charr, Laksvatn also contains anadromous brown trout (*Salmo trutta* L.) and few Atlantic salmon (*Salmo salar* L.) (Svenning *et al*., 2013). Laksvatn is connected to Balsfjord by the river Buktelva (600 m) and a shallow estuary which serves as a migratory route for anadromous Arctic charr descending from May to June and ascending in July to August. Whilst Balsfjord itself is devoid of aquaculture farming activities (Nordli *et al*., 2023), migratory Arctic charr associated with this system are known to have an intermediate to high prevalence of sea lice infection (29 to 49%), but the infection intensity is generally low (1.2 to 1.4 lice per fish, see Grenier *et al*., 2023).

Fish sampling

Our study included three life history stages of Arctic charr, parr, post-smolt and adult. Parr and adults were sampled in the lake using multi-mesh gill nets in October 2020. The nets were set overnight and consisted of 12 randomly distributed panels measuring 2.5 m in width and 1.5 m in height (with knot-to-knot sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm). The nets were set in the littoral (n = 6; 0-10 m depth), profundal (n = 4, 10-16 m depth), and pelagic zones (n = 2, 6 m deep floating net set near the surface in the deepest area of the lake).

All captured fish were frozen at -20°C until subsequent laboratory dissections. The fish were thawed, measured (fork length, mm), and weighed (g). The sagittal otoliths were extracted and preserved in ethanol for age analysis (Kristoffersen & Klemetsen, 1991). A sample of the muscle tissue was taken from the dorsal area, above the dorsal line, and re-frozen.

Fish sampled in freshwater with a length under 230 mm (Damsgård, 1991; Staurnes *et al*., 1992) and uninfected with black spot disease (*Cryptocotyle lingua*; marine skin parasite) were regarded as Arctic charr parr (see Frimeth, 1987; Kristoffersen, 1991; Kristoffersen *et al*., 1994). The other individuals caught in freshwater and infected with black spot disease or above 230 mm in length were regarded as post-migrants Arctic charr (i.e. veteran migrants). A total of 26 adults and 15 parr were collected (Table 1). Sixty-five migrants anadromous Arctic charr were captured during their returning migration between June and August using a trap in Buktelva (see trap description in Grenier, 2023) and euthanized using an overdose of benzocaine (Gontijo *et al*., 2003). Among them, 30 were caught in 2020 and 35 in 2021.

The assigned fish group was further confirmed by the estimation of the number of migrations. Grenier *et al*. (Unpublished) estimated the number of migrations for each fish using stable isotopes of sulphur ($\delta^{34}S$) and growth patterns obtained from sagittal otoliths (see detailed protocol in Grenier, 2023). The obtained number of migrations confirmed the pre- and post-migrant groupings. All the fish from the migrant group underwent one (i.e. first-time migrant) or two migrations (i.e. veteran migrant), except for two fish (with six and nine migrations) that were considered experienced veteran migrants and excluded from all subsequent analyses (Table 1 and Supplementary table S1).

Parasites examination

The fish organs were examined for metazoan parasites under a stereomicroscope. Parasites were fixed in absolute ethanol for further morphological and molecular analyses. Specimens used for the morphological analyses were whole mounts (Cribb & Bray, 2010) and identified using taxonomical criteria (e.g. Moravec, 2004). Molecular data were obtained from a subsample of specimens for each prospective parasite taxa to confirm their morphological identification. The DNA extraction, PCR amplification of the large ribosomal subunit (28S rDNA) and small ribosomal subunit (18S rDNA), sequencing analysis and phylogenetic analysis were carried out as in Rochat *et al*. (2022).

Statistical analyses

The dataset of our study included the abundance of the parasite infracommunity of 104 fish and information on all the fish hosts (age and weight). All analyses were carried out using the statistical software R version 4.2.2 (www.r-project.org). Moreover, parameters such as parasite prevalence (i.e. proportion of individuals infected in a host group) and mean abundance (i.e. mean number of parasites in a host) were calculated for each parasite species (Bush *et al*., 1997).

The difference in parasite species richness, parasite abundance between the migrants in 2020 and 2021, as well as between the fish groups, was assessed with a generalised linear models (GLM) using *stat::glm* (R Core Team, 2021). Moreover, if the parasite species richness and abundance in migrants did not differ between 2020 and 2021, the migrants 2020 and 2021 were pooled when compared to the pre- and post-migrants. The GLM models also included the weight, fish age and number of migration (for the migrants) as response variables. The weight and age variables were centred on the mean and scaled (Gelman, 2008). The models were fitted according to the data dispersion with a Poisson distribution or a Quasipoisson distribution to account for over-dispersion. Additionally, GLM analyses were carried out on the total parasite abundance, the trophically transmitted parasite abundance and the abundance of other actively transmitted parasites.

The dissimilarity in the parasite infracommunities (i.e. all the parasite individuals of one host) structure was explored, using an multidimensional scaling ordination method (MDS) *vegan:: metaMDS* (Oksanen, 2015) with Bray Curtis distance matrix, to provide an overview of the parasite infracommunities in our fish. The dissimilarity matrix was calculated upon the abundance data for each parasite species in 104 fish infracommunities. Taxa that were rarely represented in the parasite communities (overall prevalence in the dataset or subset data below 5%) and Myxozoans were excluded from this analysis as the cyst were count number of individuals.

Furthermore, a permutational multivariate analysis of variance (PERMANOVA) using *pairwise.adonis2::pairwiseAdonis* (Martinez Arbizu, 2020), was conducted to assess the impact of various factors, including fish group, fish characteristics such as weight and age, on the structure of parasite infracommunities.

Finally, all the figures were exported and further edited in Inkscape v1 for better visibility.

Results

Parasite community

A total of 22 parasite taxa were found in the 104 Arctic charr (see Table 2). Nineteen species were found in migrant Arctic charr returning from the fjord and 16 in the fish sampled in the lake (pre- and post-migrants), with an average of 9.5, 4.3 and 5.6 species respectively. Most of the parasite taxa found were endoparasites (64 %). All fish in our study harboured a least one parasite species (see Table 3); the prevalence and mean abundance of the individual parasite taxa are summarized in Table 2. *Diplostomum* sp., was the most common parasite taxa regardless of the sampling location or life history stage (prevalence of 96.0 – 100.0%).

The pre-migrants sampled in the lake were not infected with marine parasites, as they had never been to the sea. However, they were infected by nine parasite taxa from freshwater, including *Pseudocapillaria* (*Ichthyocapillaria*) *salvelini*, a nematode that was only found in pre-migrants (Table 2). Additionally, *Crepidostomum pseudofarionis*, an intestinal trematode, was exclusively found in pre- and post-migrants sampled in the lake.

The migrants caught in Buktelva were infected by eight marine parasite taxa and eleven parasite taxa from freshwater (Table 2). Overall, these anadromous Arctic charr were heavily infected by marine trematodes. For instance, the most prevalent and abundant marine parasite, *Brachyphallus crenatus* had a mean abundance between 674 and 1078 individuals per fish in 2020 and 2021 (~38 parasite individuals acquired per day). In contrast, the prevalence and mean abundance of *Abothrium gadi*, the only marine cestode, ranged between 27 (prevalence 21.4) in 2020 and 8 individuals (prevalence 11. 4%) in 2021. We also observed that some freshwater ectoparasites (i.e. *Salmincola edwardsii*) had survived the transition to freshwater on the marine migrants.

The post-migrant Arctic charr sampled in the lake had few marine parasites (three taxa, see Table 2). These marine parasites had a lower abundance and prevalence. Encysted marine parasites were in an advanced state of decomposition (e.g. *Anisakis simplex*). Post-migrants were also infected by twelve parasite taxa from freshwater. The monogenean *Discocotyle sagittata* was only found in these post-migrant Arctic charr.

Taxon richness

Parasite richness did not vary between the 2020 and 2021 Arctic charr migrants (GLM: $Z = 0.7$, P-value > 0.05; Supplementary Table S2). However, the parasite species richness differed among the three Arctic charr groups (Figure 1, Supplementary Table S2). The pre-migrants were infected by fewer parasite taxa than the migrant and post-migrant Arctic charr (GLM: pre-migrants vs migrants $Z = 6.3$, P-value < 0.001; pre-migrants vs post-migrants $Z = 2.7$, P-value = 0.008). Additionally, the parasite taxon richness was higher in migrant than post-migrant Arctic charr (GLM: post-migrants vs migrants Z-values = 4.9, P-value < 0.001).

Parasite abundance

The parasite total abundance varied between 2020 and 2021 in the migrants (GLM: $Z = 2.6$, P-value = 0.013; Table 3; Supplementary Table S3), thus, the migrants were kept in two groups when compared with pre- and post-migrants. This difference seemed to be linked with the fish weight, as bigger fish had more parasites (GLM: Z-values = 2.8, P-value = 0.006; Table 3). Additionally, more trophically transmitted parasite individuals were recorded in the migrants in 2021 and in larger fish (GLM: year $Z = 2.6$, P-value = 0.011; weight $Z = 3.0$, P-value = 0.005; Table 3), specifically the marine trematodes, but no difference was observed in the abundances of actively transmitted parasites. *Brachyphallus crenatus* and *Podocotyle atomon* had a higher abundance in 2021 than in 2020 (mean abundance of 674 in 2020 and 1078 in 2021).

Parasite abundance was greater in migrants than in pre- and post-migrants (see Table 3 and Figure 1). Migrants had more parasite individuals (1418 in 2020 and 1888 in 2021) than the post-migrants (161 parasite individuals per fish) and pre-migrants (127 parasite individuals per fish) regardless of the year (GLM: post-migrants vs migrants 2020 $Z = 7.8$, P-value < 0.001; post-migrants vs migrants 2021 $Z = 9.3$, P-value < 0.001; pre-migrants vs migrants 2020 $Z = 4.9$, P-value < 0.001; pre-migrants vs migrants 2021 $Z = 6.4$, P-value < 0.001; Supplementary Table S4). However, no significant difference in parasite abundance was found between the pre- and post-migrants (GLM: pre-migrants vs post-migrants $Z = -0.4$, P-value > 0.05). These variations in the number of parasite individuals seem to be mainly derived from the trophically transmitted parasites (see Table 3). The migrants had on average 29 times more trophically transmitted parasite individuals than fish sampled in the lake (GLM: post-migrants vs migrants 2020 $Z = 5.7$, P-value < 0.001; post-migrants vs migrants 2021 $Z = 6.5$, P-value < 0.001; pre-migrants vs migrants 2020 $Z = 4.3$, P-value < 0.001; pre-migrants vs migrants 2020 $Z = 5.6$, P-value < 0.001). In contrast, the post-migrants sampled in the lake were infected with more actively transmitted parasites than the other groups (i.e. GLM: post-migrants vs migrants 2020 $Z = -2.8$, P-value = 0.006; post-migrants vs migrants 2021 $Z = -4.5$, P-value < 0.001; post-migrants vs pre-migrants $Z = -3.0$, P-value = 0.003).

Parasite infracommunity structure

A segregation was observed in the parasite infracommunity structure among the migrants, the pre- and post-migrants sampled in the lake (Figure 2, Table 2, see pairwise.Adonis Table 3). Some fluctuation in the parasite infracommunity structure were found between the migrants from 2020 and 2021 (see pairwise.Adonis Supplementary Table S5), likely due to the higher abundance of trophically transmitted marine parasites in 2021 (Supplementary Table S3). Furthermore, larger and older fish showed a richer and more abundant parasite infracommunity which influenced the host parasite infracommunity structure (see pairwise.Adonis Table 3).

Discussion

Our study shows that sea-migrating Arctic charr had higher parasite taxa richness and abundance, especially of marine taxa, compared to pre-migrants and post-migrants caught in the lake. In particular, the abundance of trophically transmitted marine parasites was much higher in migrants than in pre- and post-migrants reflecting a marine foraging migration. The similar parasite communities in surviving individuals observed over two years suggests that the potential costs of parasitism associated with migration to the marine environment might be relatively stable between years. These patterns reveal novel insights into the dynamic interactions between migration behaviour and parasitic infections, illustrating how anadromy can significantly influence parasite load in migratory populations.

The parasite community composition we observed aligns with previous studies on Canadian anadromous Arctic charr (Bouillon & Dempson, 1989; Due & Curtis, 1995; Isinguzo, 2009), which reported similar parasite taxa (e.g. *Brachyphallus crenatus* and *Derogenes* sp.) but lower parasite abundances compared to our European migrant population (mean abundance up to 100). The higher parasite abundances in our migrants could be linked to the trophic niche of our first- and second years migrants. Notably, migrants in Canadian studies from these studies were generally larger (i.e. mean fork length from 402 up to 539 mm) than our study (i.e. mean fork length of 292 in 2020 and 329 mm in 2021). Additionally, as migrants' diets and trophic niches become specialized through repeated marine migrations, focusing on larger prey like fish, it is likely that the migrants from Canadian studies are feeding at a higher trophic level (Knudsen *et al*., 2003; Grenier *et al*., Unpublished). This contrast with the extensive feeding of first- and second-year migrants on smaller intermediate host that are likely important for trophically transmitted marine parasite.

The parasite community we observed in the marine migrants and the segregation among migrants and non-migrants of similar age and size suggests that anadromous behaviour exposes Arctic charr to two different foraging environments and the range of parasite species associated with them. In our study, trophically transmitted marine parasites dominated the communities in returning fish, reflecting the higher exposure to these parasites during the intensive feeding phase in the marine habitat. The higher abundance of marine trematodes in larger migrants further supports the role of host feeding behaviour in the acquisition of trophically transmitted parasites. On the other hand, the large-sized post-migrants sampled in the lake exhibited a higher abundance of actively transmitted parasites, indicating potential differences in transmission dynamics of these taxa between marine and freshwater environments. Moreover, host migration behaviour may also impact parasite transmission dynamics by changing the availability of suitable hosts or habitats (e.g. Aprahamian, 1985) and ecologically trapping the parasite (Remeš, 2003). A parasite acquired during its migration between two habitats can become a "dead end" if the parasites cannot complete their life cycles or reproduce within these hosts in another habitat (Torchin *et al*., 2001). Furthermore, post-migrant specimens exhibit a majority of actively transmitted parasites, including encysted forms, which are more abundant than in pre-migrants. Then, only a few trophically transmitted freshwater parasite species, indicating that post-migrant anadromous Arctic charr seem to feed to a lesser degree in freshwater once they start migrating (Young, 2019; Young & Tallman, 2021).

Three months after their return to the freshwater environment, our large-sized post-migrants harboured only two marine species (*Cryptocotyle lingua* and *Anisakis simplex* attesting their earlier marine migration (see Marcogliese & Jacobson, 2015)), and if present, they were in low abundance (less than 68.6 individuals in average). This indicate that marine parasites are either eliminated due to their salinity requirement (e.g. Zander & Reimer, 2002; Schmidt *et al*., 2003; Jakob *et al*., 2009) or have a perish at the end of their natural lifespan. This suggests that migratory escape, i.e. migrate to avoid parasites that may affect them in a particular habitat, plays a significant role in reducing parasite loads (Peacock *et al*., 2020), as the transition back to freshwater likely disrupts the life cycles of marine parasites (e.g. Bartel *et al*., 2011; Poulin *et al*., 2012). The ability to escape parasites through migration may serve as an adaptive advantage (Poulin & De Angeli Dutra, 2021), despite the costs of migration. Migration can help reduce the parasitic burden in migrants upon the transition back to freshwater as marine parasites decrease after returning to freshwater environments. This dynamic likely results in migratory recovery (Shaw & Binning, 2016), where individuals benefit physiologically from reduced parasite burdens post-migration (Poulin & De Angeli Dutra, 2021). In anadromous Arctic charr, the 'risky' feeding migration to energy- and parasite-rich marine environments and the subsequent loss of acquired parasites upon return to freshwater appears to constitute a recurring strategy. The phenomenon migratory escape will thereby lower the negative impact of the huge parasite load accumulated through the short foraging migration and be beneficial for the present anadromous Arctic charr population and for an anadromous life-history strategy in general.

This parasite community of the sea migrant Arctic charr exhibited high similarities in species richness and composition between the two successive years. This observed stability of parasite communities of mainly trophic transmitted taxa, despite some annual variations in *Brachyphallus crenatus* and *Podocotyle atomon* abundance, could suggest stability of the foraging behaviour in the fjord within the host population as well (e.g. Marcogliese, 2002; Amundsen *et al*., 2009). Our migrants rapidly accumulate a substantial parasite burden during their 44-day marine phase (Nilsen Opheim, 2022), averaging 38 established marine parasites per fish per day. Studies on salmonids showed that even a single endoparasite taxon (i.e. *Eubothrium* sp.) with low abundance can induce a reduction in its host's growth (Bristow & Berland, 1991) and impair the host's adaptation to saline conditions (Boyce & Clarke, 1983). Polyparasitic infection could be even more harmful for the host (Bordes & Morand, 2011). This because a richer parasite community has several complex interactions within the host (Cox, 2001) and can amplify detrimental effects on the host compared to single-species infections (Petney & Andrews, 1998; Bordes & Morand, 2009). Thereby a high parasitic load, consisting of up to 10 different intestinal taxa, can severely impact individual host physical condition. These mechanisms may consist of general pathogenesis from parasites (Barber *et al*., 2000; Altizer, 2001; Granroth-Wilding *et al*., 2015), impairing physiological and immune functions, reducing growth rates (e.g. Lafferty & Kuris, 2002; Moore, 2002), and increasing susceptibility to predators and environmental stressors (e.g. Lafferty & Morris, 1996; Buchmann, 1997; Berdoy *et al*., 2000; Ardia *et al*., 2011). Parasitic infections can impair a host's ability to successfully migrate (Altizer *et al*., 2011; Peacock *et al*., 2020), hindering their completion of the migratory journey and consequently impacting overall population dynamics (Bradley & Altizer, 2005; Peacock *et al*., 2018; Poulin & De Angeli Dutra, 2021).The cumulative effects of these parasitic infections not only challenge the immediate health of migratory species but also pose long-term risks to host populations through reduced survival and reproductive success.

Despite the challenges posed by high parasite burdens during the marine phase, the benefits of anadromy, such as doubling weight and therefore increasing growth (e.g. Fleming, 1996; Young *et al*., 2021; Grenier, 2023), may offset the parasitic costs of those host that survived the marine migration. The nutritional energy from feeding on richer marine prey can outweigh the potential parasitic pathogenesis costs associated with a high parasite load (Lafferty, 1992; Lafferty & Morris, 1996), especially when these can be reduced upon returning to the freshwater environment. This highlights the importance of mechanisms like migratory recovery (Shaw & Binning, 2016) and migratory culling (Bradley & Altizer, 2005). Migratory culling, i.e. selectively removing weaker infected individuals from the population, can potentially strengthen population resilience by reducing overall parasite burden (Bradley & Altizer, 2005;

Bartel *et al.*, 2011). Together, these mechanisms act as a form of natural selection (e.g. improving heritable traits as immunity), promoting traits in individuals that allow them to endure the challenges of migration and parasitism. Additionally, migrating individuals face various risks, such as predation (e.g. Krkošek *et al.*, 2007; Thorstad *et al.*, 2016), exposure to harsh environmental conditions (Hoar, 1976; Finstad *et al.*, 1989), and direct effects of parasitism such as host death (Thorstad *et al.*, 2015; Forseth *et al.*, 2017). Together, these factors can contribute to the observed high mortality rates among first-time migrants of Arctic charr (e.g. ~70%, Rikardsen *et al.*, 1997; Jensen *et al.*, 2019), However, the exact contribution to host population dynamics by the rich and abundant parasite community observed in this study remains uncertain. The removal of highly infected individuals can benefit the host population by effectively managing the parasite load within the population and promoting traits that enable individuals to endure the challenges of migration and parasitism.

Future environmental shifts due to climate change have the potential to intensify the parasitic threats and other stressors faced by migratory species (Poulin, 2006). in both freshwater and marine environments (Hoegh-Guldberg & Bruno, 2010; Woodward *et al.*, 2010). Climate change may increase parasite threats by raising the parasite load in migrant populations (Sures, 2008). Rising temperatures and changing ecological conditions, particularly in the sub-Arctic, threaten parasites and hosts by altering distribution, disrupting trophic interactions, and impacting various aspects of their biology (e.g. Marcogliese, 2001; Woodward *et al.*, 2010; Chambault *et al.*, 2020). Anadromous cold-adapted species like Arctic charr are particularly vulnerable to these temperature increases, intensifying the challenges they face (Elliott & Elliott, 2010; Svenning *et al.*, 2023). For instance, the increase in ocean temperature might expose the migratory individuals to more and/or different parasites, potentially increasing the cost of parasitism for the hosts (O'Connor & Bernhardt, 2018). Warmer temperatures directly boost parasite development and reproduction rates, while shifts in precipitation and habitat conditions expand the range and encounters of certain parasite species (e.g. Marcogliese, 2001; Lafferty, 2009). In addition to global climate change, other anthropogenic impacts, such as the expansion of fish farming and the introduction of non-indigenous species (Rolls *et al.*, 2017), could further compound these challenges by disturbing or competing with local anadromous populations (Lennox *et al.*, 2023). Overall, the cumulative effects of climate change and associated factors pose significant risks to migratory species and ecosystem dynamics. The present study in a fjord system, which is lack of aquaculture farming activities

(Nordli *et al.*, 2023), presents valuable baseline data on anadromous Arctic charr parasite communities for future assessments of such threats.

Overall, our study reveals that marine-migrating Arctic charr rapidly acquire a substantially higher burden and a more diverse parasite community compared to non-migrants. The short duration of the migration (a few weeks) and the return to the freshwater environment offer a potential escape from accumulated marine parasites that seem rapidly to succumb. However, it remains unclear to what extent parasitism contributes to the high mortality rate in migratory fish in general and anadromy specifically. This process may also function as a natural migratory culling mechanism for migrants, potentially enhancing population resilience. Climate change and other anthropogenic stressors will likely affect the dynamics between migrants and parasites, with rising temperatures and changing environmental conditions potentially amplifying the costs of parasitic infections for anadromous and other migratory fish populations in the future. Thus, although the surviving migrants sustain significant parasite infection burdens during migration, the overall benefits of enhanced growth and reproductive success, combined with mechanisms like migratory recovery, may counterbalance these parasitic costs. Our results highlight the ecological impacts of parasitism on migratory species.

Tables

Table 1: Summary of the Arctic charr sampled from Laksvatn and Buktelva in 2020 and 2021. The length, weight and age corresponding to the mean values of the fish group with its associated standard error.

	Pre migrant 2020	Migrant 2020	Migrant 2021	Post migrant 2020
Sample size (n)	15	28*	35	26
Length (mm)	211.5 (6.0)	328.5 (12.7)	291.6 (5.5)	351.6 (16.6)
Weight (g)	94.0 (8.2)	467.3 (50.3)	251.6 (14.2)	548.7 (88.0)
Age	4.3 (0.2)	5.3 (0.4)	4.1 (0.3)	5.7 (0.5)

*Two veteran’s migrants excluded from the post-smolt 2020 group (see Supplementary table S1).

Table 3: Overall parasites mean abundance (standard error) for the Arctic charr parasite community from Laksvatn and Buktelva, Norway. The dataset includes 63 migrant Arctic charr fish sampled on their return from their marine migration (returning) and 41 Arctic charr catch in the lake. The Arctic charr sampled in the lake include post migrant Arctic charr (n=26) that and pre migrant (parr n=15).

	Pre migrant 2020	Migrant 2020	Migrant 2021	Post migrant 2020	TOTAL
Trophically transmitted parasites	67.1 (14.23)	1333.5 (197.2)	1828.9 (145.7)	23.0 (6.2)	989.7 (015.8)
Actively transmitted parasites	60.1 (10.2)	84.8 (13.7)	59.1 (5.9)	137.9 (15.4)	85.0 (6.5)
All parasites pooled	127.1 (19.0)	1418.3 (195.2)	1888.0 (146.6)	161.0 (17.1)	1074.8 (104.3)

Table 2: Infection parameters for the Arctic charr parasite community from Laksvatn and Buktelva, Norway, expressed as the prevalence of infection (Prev in %), mean abundance (MA) and standard error (SE). The second column indicates the marine (M) or freshwater (F) origin of the parasite taxa. The dataset includes 63 migrant Arctic charr fish sampled on their return from their marine migration (returning) and 41 Arctic charr captured in the lake (26 post migrants and 15 pre migrants). The data on sea lice in the post smolt Arctic charr from the trap were obtained from Grenier *et al.* (2023).

Parasite taxa		Pre migrant		Migrant				Post migrant	
		2020 (n=15)		2020 (n=28)		2021 (n=35)		2020 (n=26)	
		Prev	MA (SE)	Prev	MA (SE)	Prev	MA (SE)	Prev	MA (SE)
Monogenean									
Discocotyle sagittata	F	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)	**44.0**	1.5 (0.5)
Trematoda									
Apatemon sp. ^{a}	F	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)	**2.9**	0.1 (0.1)	**8.0**	0.1 (0.1)
Brachyphallus crenatus	M	**0.0**	0.0 (0.0)	**100.0**	673.5 (89.1)	**100.0**	1077.8 (138.9)	**0.0**	0.0 (0.0)
Crepidostomum pseudofarionis	F	**33.3**	2.5 (1.8)	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)	**4.0**	0.4 (0.4)
Cryptocotyle lingua	M	**0.0**	0.0 (0.0)	**96.4**	36.5 (13.2)	**88.6**	10.5 (1.9)	**88.0**	64.7 (13.8)
Derogenes varicus	M	**0.0**	0.0 (0.0)	**100.0**	487.0 (190.3)	**100.0**	301.9 (47.9)	**0.0**	0.0 (0.0)
Diplostomum sp. ^{a}	F	**100.0**	58.7 (10.0)	**100.0**	46.4 (4.9)	**100.0**	45.3 (5.1)	**96.0**	69.8 (7.5)
Phyllodistomum umblae	F	**100.0**	10.5 (2.1)	**53.6**	2.8 (0.8)	**85.7**	10.9 (1.8)	**52.0**	3.5 (1.1)
Podocotyle atomon	M	**0.0**	0.0 (0.0)	**85.7**	41.9 (9.8)	**97.1**	351.9 (62.8)	**0.0**	0.0 (0.0)
Tylodelphys sp. ^{a}	F	**40.0**	0.7 (0.4)	**7.1**	0.1 (0.0)	**11.4**	0.1 (0.1)	**20.0**	0.3 (0.1)
Cestoda									
Abothrium gadi	M	**0.0**	0.0 (0.0)	**21.4**	26.8 (25.3)	**11.4**	7.8 (6.4)	**0.0**	0.0 (0.0)
Dibothriocephalus dendriticus & D. ditremus^{b}	F	**0.0**	0.0 (0.0)	**14.3**	1.5 (1.4)	**31.4**	2.0 (0.6)	**24.0**	4.3 (2.6)
Eubothrium salvelini	F	**13.3**	0.2 (0.1)	**21.4**	0.4 (0.2)	**45.7**	2.0 (1.1)	**12.0**	0.1 (0.1)
Proteocephalus sp.	F	**86.7**	52.5 (15.3)	**67.9**	5.4 (1.7)	**74.3**	25.7 (6.4)	**56.0**	10.6 (4.1)
Acanthocephalans									
Echinorhynchus truttae	F	**0.0**	0.0 (0.0)	**42.9**	8.9 (7.9)	**8.6**	9.2 (7.3)	**12.0**	0.1 (0.1)
Nematoda									
Anisakis simplex	M	**0.0**	0.0 (0.0)	**17.9**	0.3 (0.1)	**20.0**	0.3 (0.1)	**60.0**	3.7 (1.0)
Hysterothylacium aduncum	M	**0.0**	0.0 (0.0)	**89.3**	85.0 (17.4)	**97.1**	73.7 (9.8)	**16.0**	0.2 (0.1)

Pseudocapillaria (Ichthyocapillaria) salvelini	F	**6.7**	1.3 (1.3)	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)	**0.0**	0.0 (0.0)
Copepoda									
Salmincola edwardsii	F	**13.3**	0.2 (0.1)	**14.3**	0.2 (0.1)	**2.9**	0.0 (0.0)	**16.0**	0.2 (0.1)
Sea lice (*Lepeophtheirus salmonis salmonis* or *Caligus* sp.)[b]	M	**0.0**	0.0 (0.0)	**28.6**	0.8 (0.3)	**42.9**	1.1 (0.3)	**0.0**	0.0 (0.0)
Myxozoan									
Myxozoa gen. sp.	F	**33.3**	0.5 (0.2)	**53.6**	0.8 (0.2)	**74.3**	2.0 (0.3)	**60.0**	1.3 (0.3)
Species richness (*S*)		9		17		18		15	

[a] Prevalence and abundance estimated from a single eye.

[b] The taxa distinguishable only using microscopic techniques or molecular data were analysed together.

Table 3: Permanova on the Laksvatn parasite infracommunity between the fish group computed using *pairewiseadonis2:: pairewiseadonis2*.

	Df	Sum of squares	R2	F-values	**P-values**
Post migrant VS migrant					
Group	1	6.25	0.59	145.19	**0.001**
Weight	1	0.52	0.05	12.00	**0.001**
Age	1	0.16	0.01	3.64	**0.026**
Group: Weight	1	0.15	0.01	3.55	**0.031**
Group:Age	1	0.16	0.01	3.66	**0.017**
Residual	79	3.40	0.32		
Total	84	10.64	1.00		
Post migrant VS Pre migrant					
Group	1	1.79	0.38	29.84	**0.001**
Weight	1	0.43	0.09	7.16	**0.001**
Age	1	0.23	0.05	3.91	**0.007**
Group: Weight	1	0.07	0.01	1.12	0.347
Group:Age	1	0.08	0.02	1.26	0.281
Residual	35	2.10	0.45		
Total	40	4.69	1.00		
Migrant VS Pre migrant					
Group	1	5.27	0.65	143.62	**0.001**
Weight	1	0.17	0.02	4.71	0.022
Age	1	0.07	0.01	1.81	0.147
Group: Weight	1	0.03	0.00	0.72	0.453
Group:Age	1	0.03	0.00	0.81	0.435
Residual	68	2.49	0.31		
Total	73	8.06	1.00		

Figures

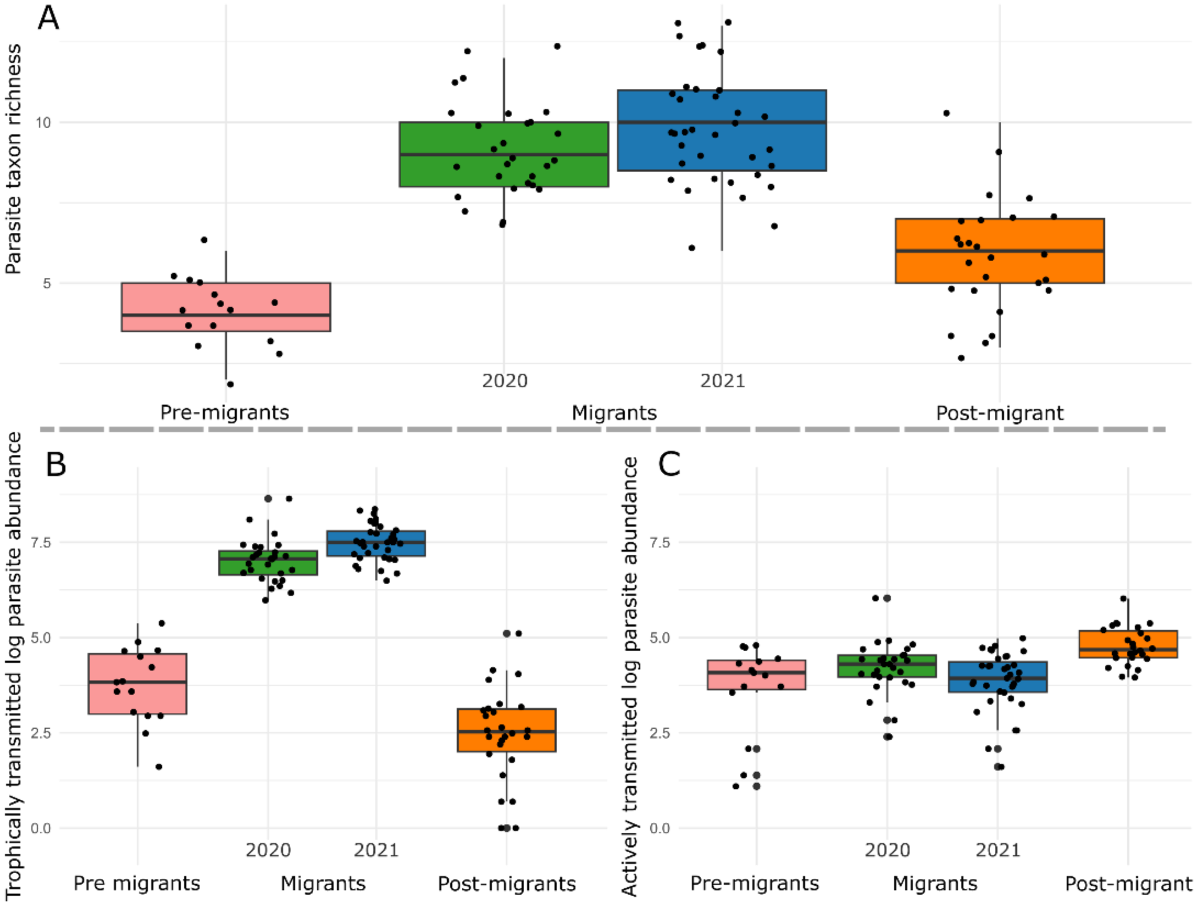

Figure 1: Boxplot of parasite richness (A) and abundance of trophically (B) and actively (C) transmitted parasites among the Arctic charr groups sampled in the lake (Pre- and Post-migrants, years pooled) and on the return migration (Migrants, 2020 in green and 2021 in blue).

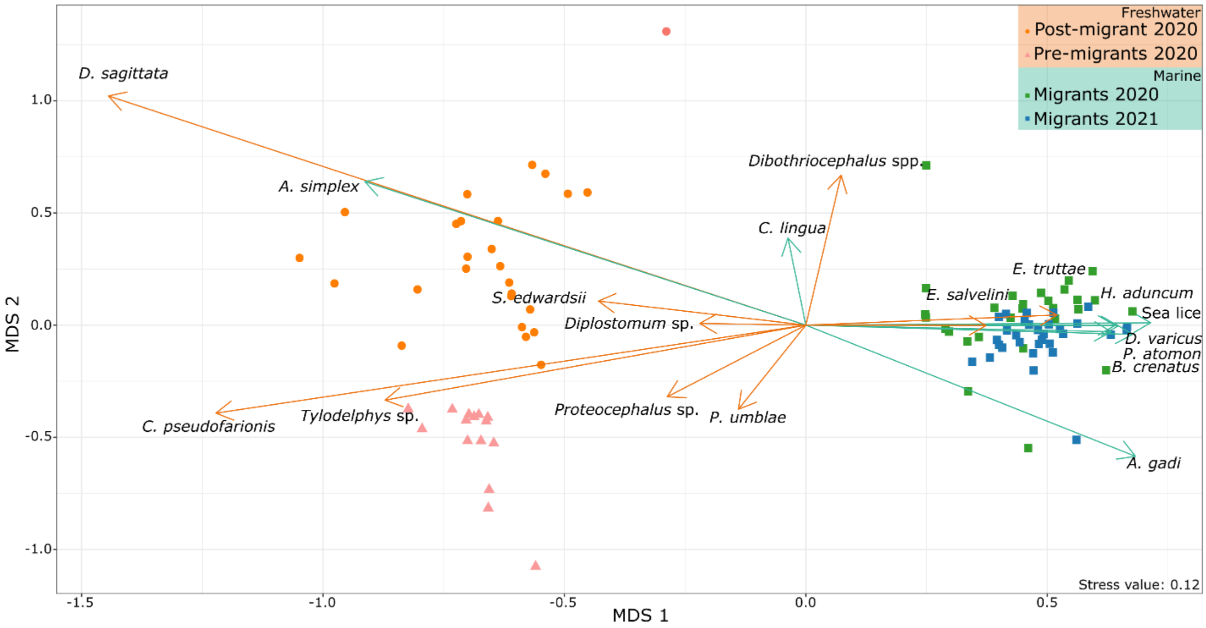

Figure 2: Multidimensional scaling biplot based on Bray–Curtis dissimilarity among parasite infracommunities through time (N=104). Infracommunities are colour-coded according to the fish group (pink, pre-migrant; green, migrant 2021; blue, migrant 2021; orange, post-migrant). The vectors with arrows indicate the contribution of each parasite taxa to the dissimilarity and colour coded according to the parasite origin (orange, freshwater and green, marine).

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Ethical statement

The animal work presented was approved by the Norwegian Animal Research Authority (2020/14374), with all field personnel having extensive experience in handling fish.

Conflict of interest

The authors declare no conflict of interest.

Data accessibility

The data that support the findings of this study are available from the corresponding author upon reasonable request. The DNA sequences will be submitted to Genbank upon manuscript submission (https://www.ncbi.nlm.nih.gov/genbank/).

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Supplementary material

Supplementary table S1: Infection parameters for two veterans migrant Arctic charr parasite community from Laksvatn, Norway, expressed as the prevalence of infection (Prev in %), mean abundance (MA) and standard error (SE). The average measurement of these two veterans were 485.0 (10.0)mmm and 1219.5 (63.5) g.

	Prev	MA (SE)
Trematoda		
Brachyphallus crenatus	100	619.5 (302.5)

Cryptocotyle lingua	50	2 (2)
Derogenes varicus	100	518.5 (3.5)
Diplostomum sp. [a]	100	31 (18)
Podocotyle atomon	100	69.5 (32.5)
Cestoda		
Proteocephalus sp.	50	0.5 (0.5)
Nematoda		
Hysterothylacium aduncum	100	300 (19)
Copepoda		
Sea lice (*Lepeophtheirus salmonis salmonis* or *Caligus* sp.)[b]	100	7.5 (0.5)
Myxozoan		
Myxozoa gen. sp.	50	1 (1)

[a] Prevalence and abundance estimated from a single eye.

[b] The taxa distinguishable only using microscopic techniques or molecular data were analysed together.

Supplementary table S2: GLM analysis on the parasite species richness among fish group

	Estimate	Standard error	Z-value	P-value
Migrant 2020 VS Migrant 2021				
(Intercept)	-130.42	194.29	-0.67	0.502
Year	0.07	0.10	0.68	0.495
Age	-0.03	0.08	-0.31	0.757
Weight	0.01	0.12	0.11	0.912
Pre migrant VS Migrant VS Post migrant				
(Intercept - post migrant)	1.79	0.08	21.34	**< 2e-16**
Pre migrant	-0.44	0.17	-2.65	**0.008**
Migrant	0.46	0.09	4.90	**9.43E-07**
(Intercept pre migrant)	1.35	0.14	9.85	**< 2e-16**
Post migrant	0.44	0.17	2.65	**0.008**
Migrant	0.90	0.14	6.35	**2.22E-10**
Age	0.02	0.07	0.27	0.787
Weight	-0.07	0.08	-0.94	0.348

Supplementary table S3: GLM analysis on the parasite abundance in migrant Arctic charr through time.

	Estimate	Standard error	Z-value	P-value
Parasite abundance				
(Intercept)	-1045.00	-1045.00	-2.56	**0.013**
Year	0.52	0.52	2.58	**0.013**
Number of migration	-0.25	-0.25	-1.00	0.323
Age	-0.04	-0.04	-0.33	0.744
Weight	1166.00	1166.00	1.53	0.133
Year:Weight	-0.58	-0.58	-1.53	0.133
Trophically transmitted parasite abundance				
(Intercept)	-1120.00	427.60	-2.62	**0.011**
Year	0.56	0.21	2.64	**0.011**
Number of migration	-0.25	0.26	-0.96	0.340
Age	-0.04	0.14	-0.26	0.797
Weight	1235.00	795.80	1.55	0.126
Year:Weight	-0.61	0.39	-1.55	0.126

Actively transmitted parasite abundance				
(Intercept)	361.1157	554.5721	0.65	0.518
Year	-0.1765	0.2746	-0.64	0.523
Number of migration	-0.175	0.3342	-0.52	0.603
Age	-0.2192	0.1901	-1.15	0.254
Weight	-380.4846	1128.4046	-0.34	0.737
Year:Weight	0.1886	0.5586	0.34	0.737

Supplementary table S4: GLM analysis on the parasite abundance amoong fish group.

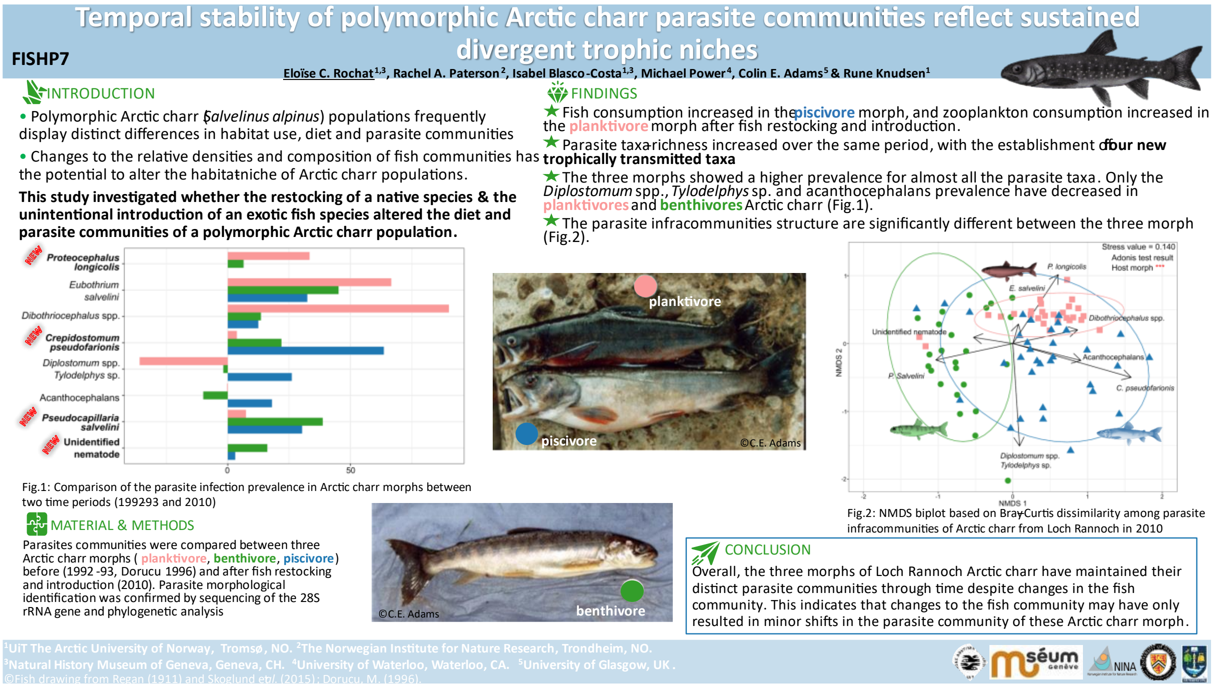
	Estimate	Standard error	Z-value	P-value
Parasite abundance				
(Intercept pre migrant)	5.04	0.42	12.07	**< 2e-16**
Post migrant	-0.20	0.52	-0.38	0.705
Migrant 2020	2.12	0.44	4.86	**4.44E-06**
Migrant 2021	2.68	0.42	6.39	**5.52E-09**
(Intercept post migrant)	4.85	0.29	16.56	**< 2e-16**
Migrant 2021	2.88	0.31	9.30	**3.97E-15**
Migrant 2020	2.32	0.30	7.82	**6.10E-12**
Pre migrant	0.20	0.52	0.38	0.705
Age	0.01	0.10	0.10	0.924
Weight	0.26	0.13	2.01	**0.047**
Trophically transmitted parasite abundance				
(Intercept pre migrant)	4.45	0.58	7.62	**1.60E-11**
Post migrant	-1.64	0.96	-1.71	**9.11E-02**
Migrant 2020	2.61	0.60	4.34	**3.43E-05**
Migrant 2021	3.27	0.58	5.60	**1.98E-07**
(Intercept post migrant)	2.81	0.74	3.78	**2.68E-04**
Migrant 2021	4.91	0.75	6.52	**3.14E-09**
Migrant 2020	4.25	0.74	5.72	**1.15E-07**
Pre migrant	1.64	0.96	1.71	0.091
Age	-0.01	0.11	-0.07	0.943
Weight	0.35	0.15	2.34	0.021
Actively transmitted parasite abundance				
(Intercept pre migrant)	4.13	0.22	19.07	**< 2e-16**
Post migrant	0.76	0.25	3.01	**0.003**
Migrant 2020	0.30	0.26	1.16	0.250
Migrant 2021	-0.06	0.25	-0.24	0.809
(Intercept post migrant)	4.89	0.11	44.06	**< 2e-16**
Migrant 2021	-0.82	0.18	-4.50	**1.87E-05**
Migrant 2020	-0.46	0.17	-2.80	**0.006**
Pre migrant	-0.76	0.25	-3.01	**0.003**
Age	-0.11	0.12	-0.89	0.373
Weight	0.09	0.12	0.80	0.424

Supplementary table S5: Permanova on the Laksvatn parasite infracommunity between the fish group computed using *pairewiseadonis2:: pairewiseadonis2*.

	Df	Sum of squares	R2	F-values	**P-values**
Post migrant VS migrant 2020					
Group	1	4.29	0.56	89.03	**0.001**
Weight	1	0.50	0.06	10.37	**0.001**

Age	1	0.20	0.03	4.23	**0.018**
Group: Weight	1	0.25	0.03	5.14	**0.007**
Group:Age	1	0.14	0.02	2.88	**0.039**
Residual	48	2.31	0.30		
Total	53	7.70	1.00		
Post migrant VS migrant 2021					
Group	1	5.34	0.64	121.03	**0.001**
Weight	1	0.44	0.05	10.01	**0.001**
Age	1	0.21	0.03	4.86	**0.015**
Group: Weight	1	0.00	0.00	0.8	0.969
Group:Age	1	0.12	0.01	2.71	0.063
Residual	51	2.25	0.27		
Total	56	8.37	1.00		
Post migrant VS Pre migrant					
Group	1	1.79	0.38	29.84	**0.001**
Weight	1	0.43	0.09	7.16	**0.002**
Age	1	0.23	0.05	3.91	**0.015**
Group: Weight	1	0.07	0.01	1.12	0.340
Group:Age	1	0.08	0.02	1.26	0.293
Residual	35	2.10	0.45		
Total	40	4.69	1.00		
Migrant 2020 VS Pre migrant					
Group	1	4.47	0.71	117.29	**0.001**
Weight	1	0.22	0.04	5.90	**0.011**
Age	1	0.12	0.19	3.18	**0.037**
Group: Weight	1	0.02	0.00	0.56	0.570
Group:Age	1	0.04	0.01	0.93	0.404
Residual	37	1.41	0.22		
Total	42	6.28	1.00		
Migrant 2021 VS Pre migrant					
Group	1	4.36	0.075	129.77	**0.001**
Weight	1	0.01	0.00	0.42	0.676
Age	1	0.02	0.00	0.49	0.596
Group: Weight	1	0.03	0.01	0.89	0.388
Group:Age	1	0.03	0.01	0.91	0.384
Residual	40	1.35	0.23		
Total	45	5.80	1.00		
Migrant 2020 VS Migrant 2020					
Group	1	0.20	0.09	6.68	**0.001**
Weight	1	0.22	0.10	7.59	**0.001**
Age	1	0.07	0.03	2.38	**0.034**
Group: Weight	1	0.02	0.01	0.78	0.574
Group:Age	1	0.06	0.03	1.99	0.067
Residual	53	1.56	0.73		
Total	58	2.13	1.00		

Posters



Temporal stability of polymorphic Arctic charr parasite communities reflect sustained divergent trophic niches

FISHP7

Eloïse C. Rochat[1,3], Rachel A. Paterson[2], Isabel Blasco-Costa[1,3], Michael Power[4], Colin E. Adams[5] & Rune Knudsen[1]

INTRODUCTION

- Polymorphic Arctic charr (*Salvelinus alpinus*) populations frequently display distinct differences in habitat use, diet and parasite communities
- Changes to the relative densities and composition of fish communities has the potential to alter the habitat-niche of Arctic charr populations.

This study investigated whether the restocking of a native species & the unintentional introduction of an exotic fish species altered the diet and parasite communities of a polymorphic Arctic charr population.

Fig.1: Comparison of the parasite infection prevalence in Arctic charr morphs between two time periods (1992-93 and 2010)

MATERIAL & METHODS

Parasites communities were compared between three Arctic charr morphs (planktivore, **benthivore**, **piscivore**) before (1992 -93, Dorucu 1996) and after fish restocking and introduction (2010). Parasite morphological identification was confirmed by sequencing of the 28S rRNA gene and phylogenetic analysis

FINDINGS

★ Fish consumption increased in the **piscivore** morph, and zooplankton consumption increased in the **planktivore** morph after fish restocking and introduction.

★ Parasite taxa-richness increased over the same period, with the establishment of **four new trophically transmitted taxa**

★ The three morphs showed a higher prevalence for almost all the parasite taxa. Only the *Diplostomum* spp., *Tylodelphys* sp. and acanthocephalans prevalence have decreased in **planktivores** and **benthivores** Arctic charr (Fig.1).

★ The parasite infracommunities structure are significantly different between the three morph (Fig.2).

Fig.2: NMDS biplot based on Bray-Curtis dissimilarity among parasite infracommunities of Arctic charr from Loch Rannoch in 2010

CONCLUSION

Overall, the three morphs of Loch Rannoch Arctic charr have maintained their distinct parasite communities through time despite changes in the fish community. This indicates that changes to the fish community may have only resulted in minor shifts in the parasite community of these Arctic charr morph.

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©Fish drawing from Regan (1911) and Skoglund et al. (2015); Dorucu, M. (1996).

Poster: Rochat, Paterson, Blasco Costa, Power, Adams & Knudsen (2021). "Parasite infections in anadromous Arctic charr from Northern Norway." 13th European Multicolloquium of Parasitology.

Parasite infections in anadromous Arctic charr from Northern Norway

Eloïse C. Rochat, Hedda A. Nilsen, Gabrielle Grenier & Rune Knudsen

PO15

CHARR 2023 JAPAN

Introduction:

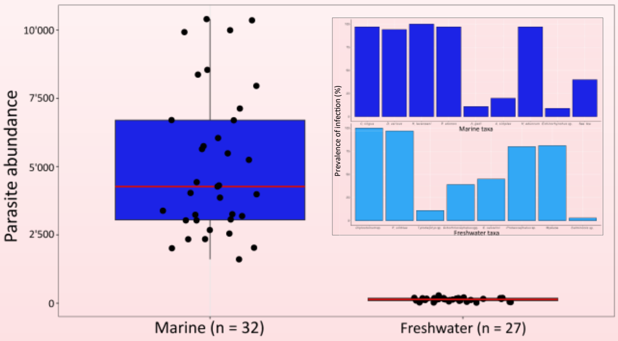
Anadromous charr can acquire parasites in two different environments, the **freshwater** and the **marine** systems. **Parasites** have **negative effects** on their host at the individual and population levels.

In recent years, populations of anadromous Arctic charr have declined in northern Norway and the Arctic region.

Parasite - the cost of anadromy?

Material & Methods:

Sea-running post-smolts of Arctic charr were collected (1’125 in 2020 and 1’518 in 2021) after their sea-migration period using a trap in the river near Lake Laksvatn, northern Norway, in a fjord without aquaculture activity. The parasite communities, diet, and stable isotopes (δ13C, δ15N and δ34S) from 32 fish were evaluated.



Findings:

- **High abundance of marine parasites** (mean abundance > 5’000) and **high species richness**
- Even number of marine and freshwater parasites species
- Majority are **trophically transmitted parasites** (from prey items)
- **Parasites**, **stomach content** and **stable isotopes** data support feeding on marine prey

prevalence - number of infected fish with a particular parasite in %
abundance - number of parasites individuals per fish

Conclusions:

Our results show an **excessive abundance** and **biomass of marine parasites** infecting sea-running Arctic charr. These high infection levels could be an important contribution to the low post-smolt survival during their first year of sea migration.

Therefore, these vulnerable anadromous Arctic charr populations could be at further risk if their parasite load increase in the fjord caused by climate change or other anthropogenic-induced multiple stressors.

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Poster: Rochat, Auestad Nilsen, Grenier & Knudsen (2023). "Parasite infections in anadromous Arctic charr from Northern Norway." 10th International Charr Symposium.