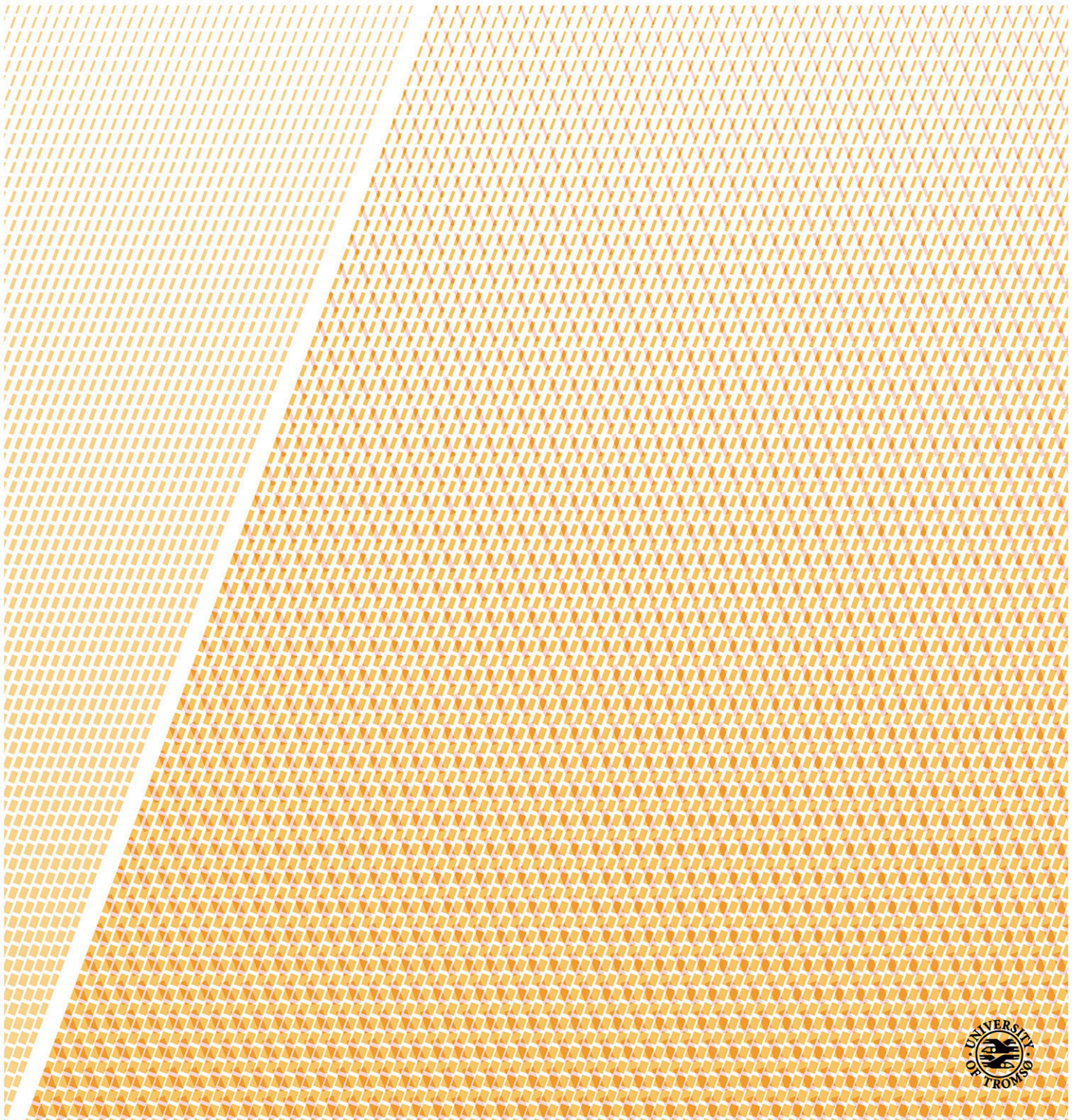


Spatial and temporal variations in parasite communities of freshwater fish in the subarctic

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A dissertation for the degree of Philosophiae Doctor – summer 2015



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Summary

Parasite communities are complicated systems believed to be affected by multiple ecological and environmental factors, both in time and space. These communities might be disrupted by anthropogenic host introductions which unfortunately appear to be a common practice e.g. in freshwater fish management. By addressing parasite occurrences in three of the most common freshwater fish species in subarctic lakes of Northern Europe; brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*) and three-spined stickleback (*Gasterosteus aculeatus*), we sought to increase the knowledge regarding how these complicated systems vary and how they might be affected by a possible host introduction. The main aim of this PhD thesis was therefore to study the spatial and temporal differences and changes in parasite occurrences in freshwater fish from northern Norway, and also to explore the importance of three-spined stickleback as a tentative transmission host for salmonid fishes.

By comparing the parasite community of an introduced three-spined stickleback population in comparison with the nearby source population, an overall high similarity was observed between the two systems. This suggests that parasite occurrences can be expected to be similar in locally separated ecosystems, as long as important environmental variables are similar. Additionally, a high degree of successful parasite introductions and establishment suggests that concomitant parasite introductions should be anticipated when new host species are introduced into an ecosystem on a small spatial scale. In addition to introducing new parasite species, introduction of a host species may also create additional host links in the food web of the recipient ecosystem which possibly aid other parasite species, such as trophically transmitted generalist parasites, to increase in occurrence.

An introduced host species might additionally function as a new prey item with potential importance to the parasite infra- and component populations of piscivorous fish species in the recipient ecosystem. By analyzing the importance of available prey fish for the transmission of *Diphyllbothrium* spp. to piscivorous brown trout, it was observed that the *Diphyllbothrium* infections increased in trout when sympatric fish species were present. Particularly high infections occurred when brown trout had the opportunity to prey on three-spined stickleback. These findings indicate that by introducing a prey fish, which feeds extensively on the first intermediate host of a trophically transmitted parasite species, into an ecosystem with a piscivorous fish population, in which there is almost absent utilization of that intermediate host, underused transmission links in the food web can be bypassed. Consequently, parasite transmission may flow through the newly introduced trophical node (the fish prey) causing an increase in parasite host links and in the occurrence of the parasite species.

Investigating within-ecosystem variation in the parasite infracommunity composition of a host species further helped to understand the impact that host introduction and manipulation might have on an ecosystem. Overall stability was observed when exploring long-term temporal and spatial variation in the intestinal parasite infracommunities of an Arctic charr population. Long-term temporal variation was absent, indicating that the infracommunities were in an overall steady state, and spatial stability was present in the form of similar infracommunity composition between individual charr. Helminth endoparasite communities of freshwater fish are considered inherently unstable, as no regulating factors are usually identified. Observed stability likely comes from environmentally stable biotic and abiotic factors. An unregulated parasite community would likely experience large changes following a perturbation such as the introduction of a new host species and associated parasites. This again stress the severity of a host introduction.

Even though parasite communities are complex ecological entities, the present study demonstrate that a great degree of similarity, predictability and stability can be observed in parasite communities of freshwater fish in northern Norway. In addition, three-spined stickleback was found as expected to play an important role in the occurrences of various parasite species emphasizing the ecological importance of this fish species. Its high impact on the structure and functionality of ecological food webs and parasite communities therefore strongly advises to discourage the practice of introducing this host species.

List of papers

This PhD thesis is based on the following papers, which are referred to by their Roman numerals:

Paper I

Jesper A. Kuhn, Roar Kristoffersen, Rune Knudsen, Jonas Jakobsen, David J. Marcogliese, Sean A. Locke, Raul Primicerio and Per-Arne Amundsen

Parasite communities of two three-spined stickleback populations in subarctic Norway—effects of a small spatial-scale host introduction

Parasitology Research (2015). DOI 10.1007/s00436-015-4309-2

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Paper II

Jesper A. Kuhn, André Frainer, Rune Knudsen, Roar Kristoffersen and Per-Arne Amundsen

Effects of fish species composition on *Diphyllbothrium* spp. infections in subarctic brown trout - is three-spined stickleback a key species?

Manuscript

Paper III

Jesper A. Kuhn, Rune Knudsen, Roar Kristoffersen, Raul Primicerio and Per-Arne Amundsen

Temporal changes and structural variation in the intestinal parasite community of Arctic charr in a subarctic lake

Manuscript

List of papers and contributions (co-author statements)

Name of candidate: Jesper Andreas Kuhn

Papers

The following papers are included in my PhD thesis:

I: Jesper A. Kuhn, Roar Kristoffersen, Rune Knudsen, Jonas Jakobsen, David J. Marcogliese, Sean A. Locke, Raul Primicerio, Per-Arne Amundsen. Parasite communities of two three-spined stickleback populations in subarctic Norway—effects of a small spatial-scale host introduction


II: Jesper A. Kuhn, André Frainer, Rune Knudsen, Roar Kristoffersen, Per-Arne Amundsen. Effects of fish species composition on *Diphyllbothrium* spp. infections in subarctic brown trout - is three-spined stickleback a key species?

III: Jesper A. Kuhn, Rune Knudsen, Roar Kristoffersen, Raul Primicerio, Per-Arne Amundsen. Temporal changes and structural variation in the intestinal parasite community of Arctic charr in a subarctic lake

Contributions in alphabetical order

	Paper I	Paper II	Paper III
Concept and idea	PAA, RoK	JK, PAA	JK, PAA
Study design and methods	JJ, JK, RoK	JK, PAA, RoK, RuK	JK, PAA, RoK, RuK
Data gathering and interpretation	JJ, JK, PAA, RoK, RP, RuK, SAL	AF, JK, PAA, RoK, RuK	JK, PAA, RoK, RP, RuK
Manuscript preparation	DJM, JK, PAA, RoK, RuK, SAL	AF, JK, PAA, RoK, RuK	JK, PAA, RoK, RuK


With my signature I consent that the above listed articles where I am a co-author can be a part of the PhD thesis of the PhD candidate.


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Roar Kristoffersen



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Introduction

The increasing awareness of the importance of parasites in ecology is partly credited to publications pleading for their recognition (Marcogliese and Cone 1997; Lafferty et al. 2008; Byers 2009). Studies have now demonstrated the ecological importance of parasites, especially concerning their involvement in the structuring of ecological food webs (Tompkins and Begon 1999; Dobson et al. 2008; Amundsen et al. 2009; Amundsen et al. 2013). Classically, parasites are defined as organisms that live on, off and at the expense of another organism, a so-called host (Esch and Fernández 1993). In most cases when a parasite is successfully introduced to a host, it is restricted to the physical extensions of that host. Further dispersion of the parasite therefore depends on the movement and migration of the infected host, at times aided along by anthropogenic host introduction. Individual hosts are complicated systems which in many ways resemble that of a miniature ecosystem (Rynkiewicz et al. 2015) and can thus be infected with multiple parasite species forming a parasite community (Dobson et al. 2008). Parasite communities are complex structures that are under regulation by several different abiotic and biotic factors in both space and time (Holmes 1987; Holmes 1990) and might be greatly affected by anthropogenic host introduction. Parasitological studies on various population and community levels, in both time and space, will increase our knowledge regarding the occurrence of parasites. This may aid in drawing more general conclusions regarding parasite ecology and the role of parasites in food webs as well as ecosystem functioning and the possible effects of anthropogenic host introduction.

Parasite introduction and establishment

Fish are often hosts to a number of parasite species (Dobson et al. 2008). Both globally and locally, anthropogenic fish introduction is a common phenomenon (Kolar and Lodge 2002; Garcia-Berthou et al. 2005). In this process, parasites might be brought along, as introduced hosts can be infected with various parasites (Williamson 1996; Daszak 2000; Cleaveland et al. 2002). Most studies deal with exotic species and host introduction on a large geographical scale (Poulin and Mouillot 2003; Kelly et al. 2009; Vignon et al. 2009; Lymbery et al. 2010; Roche et al. 2010; Gendron et al. 2012). Few studies have, in contrast, addressed the effects of host introduction on a small geographical scale (e.g. local introduction), even though successful dispersal is more likely to occur on this scale, particularly for species with a life cycle that otherwise may limit their dispersal to other habitats or ecosystems.

Introduced hosts often have depauperate parasite infracommunities in comparison to those found in their original population, as some parasites are not brought along with the introduction or may fail to establish in the new habitat (MacLeod et al. 2010). Successful introduction of a parasite species is partly dependent on its dispersal capability and lifecycle

strategy. “Allogenic” freshwater fish parasites complete their lifecycle within an aquatic ecosystem using fish as final host and thus have a limited dispersal capability (Esch et al. 1988). Parasites with an “allogenic” lifecycle, on the other hand, exploit terrestrial mammalian or avian species as final hosts that gives them a good dispersal capability as their eggs are dispersed between lakes and across large geographical distances (Esch et al. 1988). Anthropogenic host introduction reduces these differences in dispersal capabilities and may introduce parasites, which would otherwise not be naturally dispersed between ecosystems.

When a parasite is introduced, successful establishment also partly depends on the lifecycle strategy of that parasite. “Specialist” parasites infect only one or a few host species, whereas “generalist” parasites can infect a much larger range of hosts (Bush and Kennedy 1994; Poulin and Morand 2004). The probability of encountering a suitable host is therefore higher for generalist parasites, thus increasing their chance of successful colonization.

Successful colonization and overall occurrences of already established parasites might also depend on biotic and abiotic factors (Dobson 1990; Marcogliese and Cone 1996; Takemoto et al. 2005; Poulin 2007; Kennedy 2009; Poulin et al. 2011; Karvonen et al. 2013). Such factors likely vary through geographical space, which could explain why parasite community similarity generally decreases with increasing geographical distance (Poulin and Morand 1999; Poulin 2003; Perez-del-Olmo et al. 2009; Locke et al. 2012). Habitats separated by small geographical distances would thus presumably have similar biotic and abiotic factors possibly leading to high similarity between parasite communities.

The three-spined stickleback (*Gasterosteus aculeatus* L.) is commonly infected with a wide range of parasites (Zander 2007; Barber 2013). In northern Norway, this fish species was deliberately introduced to Lake Takvatn from the nearby Lake Sagelvatn (Jørgensen and Klemetsen 1995) which presents a model system useful for studying spatial differences in the occurrence of parasites on a small spatial scale, parasite introduction and overall effects of host introduction on the recipient ecosystem.

The importance of sympatric fish species

The importance of sympatric fish species for the composition of parasite communities in freshwater fish have been emphasized (Halvorsen 1971; Wootton 1973; Kennedy 1990; Marcogliese and Cone 1991; Fernández et al. 2010).

Brown trout (*Salmo trutta* L.), Arctic charr (*Salvelinus alpinus* (L.)) and three-spined stickleback are widespread freshwater fish species (Wootton 1984; Klemetsen et al. 2003). In northern Scandinavia, three-spined sticklebacks are normally associated with the littoral zone where they, among other prey items, feed on zooplankton (Langeland 1982; Wootton 1984; Jørgensen and Klemetsen 1995). Allopatric brown trout normally reside in the littoral zone feeding on benthic prey (Klemetsen et al. 2003; Knudsen et al. 2008). In sympatry with Arctic charr, brown trout typically dominate the littoral zone where they feed not only on benthic

prey and surface insects, but also on fish (Jansen et al. 2002; Sánchez-Hernández and Amundsen 2015). Arctic charr are pushed to the pelagic zone, where they feed extensively on zooplankton (Langeland et al. 1991; Knudsen et al. 2008; Eloranta et al. 2013; Skoglund et al. 2013).

Turning to piscivory effectively increases energy intake (Keast 1985; Mittelbach and Persson 1998; Elliott and Hurley 2000), but may also lead to increased parasite infections as some fish parasites can be transmitted from the fish prey to the fish predator (Williams and Jones 1994; Valtonen and Julkunen 1995). As piscivory is more common when suitable fish prey species are available (L'Abée-Lund et al. 1992; L'Abée-Lund et al. 2002), the parasite infections in a piscivorous fish is likely related to the fish composition of its habitat.

The parasite genus *Diphyllbothrium* is distributed in circumpolar regions and includes the most important fish-borne zoonosis among the cestode parasites (Dick et al. 2001; Chai et al. 2005; Scholz et al. 2009). It commonly infects brown trout, Arctic charr and three-spined stickleback in northern Europe (Halvorsen 1970; Henricson 1977; Andersen and Valtonen 1992; Rahkonen and Koski 1997; Knudsen et al. 2008). Copepods are utilized as first intermediate hosts, fish as second intermediate hosts and typically birds as final hosts (Vik 1964; Halvorsen 1970; Bakke 1985). This genus possesses the ability to transmit from fish prey to fish predator (Vik 1964; Halvorsen and Wissler 1973; Curtis 1984). Arctic charr and three-spined sticklebacks are highly susceptible to infection by *Diphyllbothrium* spp. larvae as they may feed extensively on zooplankton, including copepods. Brown trout, on the other hand, may alternatively become exposed through their piscivorous behavior.

Three-spined sticklebacks are common fish prey for subarctic salmonids (L'Abée-Lund et al. 1992; Amundsen 1994; Knudsen et al. 2008; Eloranta et al. 2013). Brown trout, in particular, are known to feed frequently on sticklebacks (L'Abée-Lund et al. 1992; Knudsen et al. 2008; Eloranta et al. 2013) but may also prey on Arctic charr (L'Abée-Lund et al. 1992; Damsgård and Langeland 1994; Knudsen et al. 2008). Targeting fish species, and in particular three-spined sticklebacks as prey, might very well be the reason for the elevated parasite infections observed in piscivorous salmonids (Knudsen et al. 1996; Knudsen et al. 2008) which thus stresses the potential effects of anthropogenic host introduction.

By comparing lakes in northern Norway with contrasting fish species compositions, the importance of sympatric fish species on the *Diphyllbothrium* spp. infections in brown trout could be addressed, predicting additional effects following a host introduction.

Long-term temporal and spatial variation between infracommunities

To clarify how severely a host introduction might alter a recipient ecosystem, knowledge regarding how much variation is already present within the ecosystem is needed.

Although strong individual feeding specializations can be observed, Arctic charr is considered to be an opportunistic feeder as most major prey items in the habitat are utilized (Johnson 1980; Amundsen 1995; Klemetsen et al. 2003). This makes it exposed to a wide range of

trophically transmitted parasite species. In northern Norway, more than 10 different macroparasite species have been reported to infect Arctic charr (Kristoffersen 1995). Four of these have their adult stage in the intestine, including the three cestode taxa *Eubothrium salvelini*, *Cyathocephalus truncatus* and *Proteocephalus* sp., and one trematode taxa *Crepidostomum* spp. (Knudsen 1995; Sterud 1999). Copepods are used as intermediate host by *E. salvelini* and *Proteocephalus* sp., whereas *C. truncatus* use amphipods (*Gammarus lacustris*) (Vik 1958; Vik 1963; Boyce 1974; Sysoev et al. 1992; Scholz 1999). *Crepidostomum* spp., on the other hand, use molluscs such as the mussel genus *Pisidium* or the snail genus *Lymnaea* as first intermediate hosts and amphipods or aquatic insect larvae as second intermediate hosts (Thomas 1958; Awachie 1968). With such complexity in the lifecycles of these parasites, the composition of the intestinal parasite infracommunity in Arctic charr is likely dependent on several factors. Pre-infection factors such as the density of intermediate hosts and host feeding behavior might control how exposed a host is to specific parasite taxa, whereas post-transmission factors such as individual host immune responses and intra- and inter-specific competition between parasites might affect the degree of infection.

Several biotic and abiotic factors likely influence the structure of parasite communities (Holmes 1987; Holmes 1990) both spatially and temporally. Seasonal fluctuations in the occurrence of parasites are found in many parasite-host systems (Scott and Smith 1994), which is not surprising as influential factors likely fluctuate seasonally themselves. A parasite-host system under seasonal change, often returns to an overall equilibrium, causing static behavior in the occurrence of parasites on a temporal scale (Scott and Smith 1994). Studies on long-term temporal changes in the occurrence of intestinal parasites in salmonids are few (Knudsen et al. 2002), most likely due to the extensive and time-consuming labor of collecting and processing the biological material. On a short-term temporal scale, the occurrences of helminth endoparasite in freshwater fishes are reported to be inherently unstable (Kennedy and Rumpus 1977). It is thus possible that on a more long-term scale (i.e., several years), these systems might show long-term variation. In the intestinal parasite infracommunity of Arctic charr, possible temporal changes in pre- and post-transmission factors could likely cause such long-term variation. Investigating whether significant and persistent temporal fluctuations in infracommunities are present, will help us to increase our knowledge regarding the dynamics of these complex systems and assess the impact that potential host introduction might have.

Objectives

The overall aim of this PhD thesis was to study the spatial and temporal variation in the occurrence of freshwater fish parasites in northern Norway, in order to assess the possible consequences following host introduction. In particular, the purpose was to understand the possible impact of introducing three-spined stickleback on a small spatial scale and the effects the presence of this fish species might have on a recipient ecosystem.

Main objectives:

1. Compare the metazoan parasite communities of an introduced stickleback population with that of the nearby source population, in order to address how host introduction on a small spatial scale might introduce parasites and what potential effects this might have on the recipient ecosystem (Paper I).
2. Analyze what importance the fish species composition of an ecosystem has on the occurrence of a trophically transmitted parasite species, using brown trout and *Diphyllbothrium* spp. as the model host-parasite system, while emphasizing the importance of the presence of three-spined stickleback as prey (Paper II).
3. Explore potential resilience in the parasite community of an Arctic charr population by studying the presence of temporal and spatial variation in the form of long-term changes in the occurrence of intestinal parasites and differences in intestinal parasite composition between individual hosts (Paper III).

(see summary of papers for additional hypotheses)

Methods

This PhD thesis is based on extensive fish sampling, parasite retrieval and identification, covering nine lakes in northern Norway (see Figure 1).

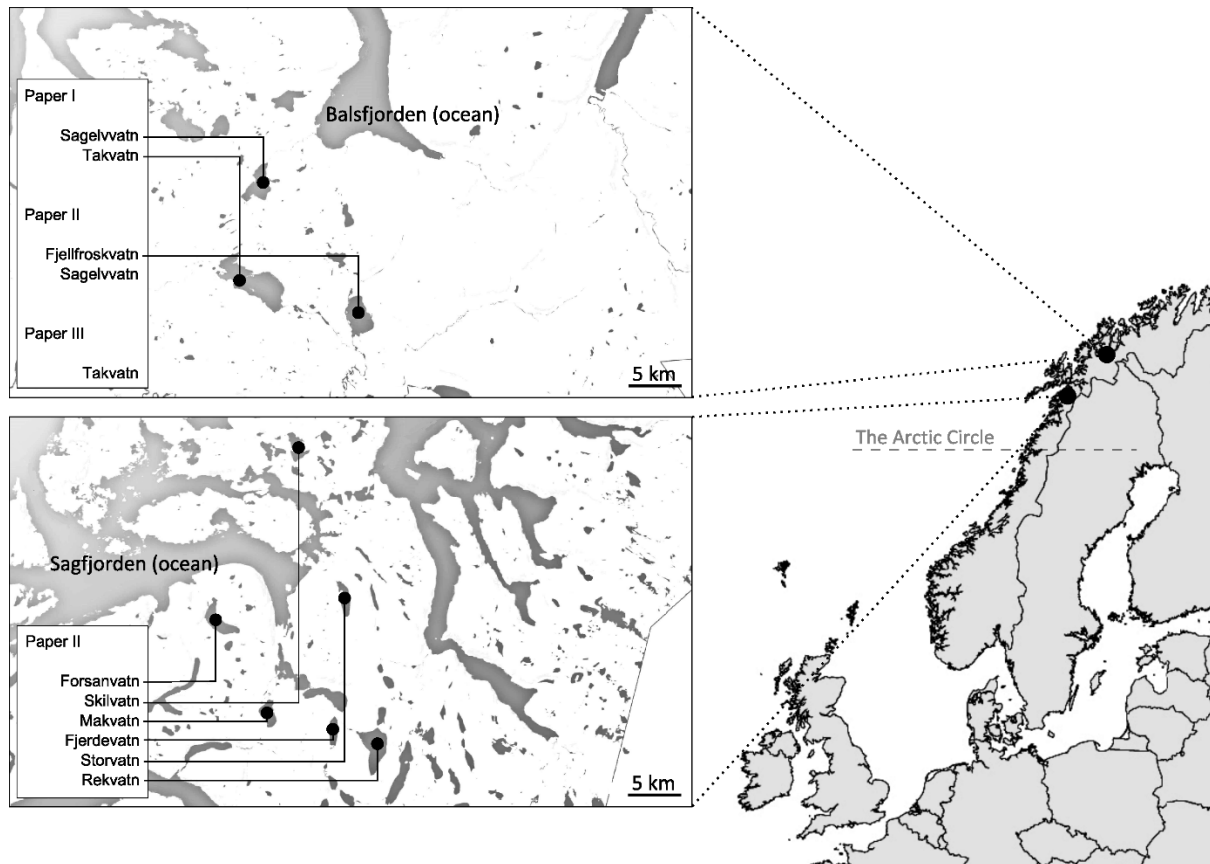


Figure 1. Map showing locations of the nine lakes sampled as part of this PhD thesis and their affiliations with Paper I, II and III.

The same fishing procedures were implemented in all lakes and years sampled as part of the data collection of the papers included in this PhD thesis. Multi-mesh survey gillnets (mesh sizes 10 to 45 mm, knot to knot) were put out overnight in the littoral zone (1 - 10 meters depth), the profundal zone (> 20 meters depth) and the pelagic zones (0 - 6 meters) for approximately 12 hours. In the case of study designs involving sampling for three-spined stickleback, 6 – 8 mm mesh-size gill nets as well as occasional minnow traps were put out in the littoral zone.

The majority of the parasite species included in this thesis are already known from the geographical region (Knudsen 1995; Kristoffersen 1995; Amundsen et al. 2013). Parasite identification to genera and in some cases species level could therefore generally be obtained

in the field based on prior knowledge and external morphological features observable using stereo microscopy on 64 x – 400 x magnification. In Paper I, complicated genetic methods were however necessary to clarify a multiple species complex regarding eye trematodes in three-spined stickleback. Thorough descriptions of the genetic techniques can be found in the method section of that paper.

Parasite retrieval

Three different ways of parasite retrieval were used in the three papers included in this PhD thesis.

Paper I aimed at a more or less complete screening of the metazoan parasite species infecting three-spine sticklebacks, including ectoparasites. As the parasite infection of individual sticklebacks were of importance, the fish were kept separately by removing them from the gill net, euthanizing them and then keeping them in individual glass vials filled with water. This way the individual parasite community of each fish could be studied. Further procedure included a complete screening for ectoparasites followed by a thorough examination for endoparasites while keeping the fish in a petridish filled with physiological saltwater (9%). This had no effect on the counting of ectoparasites and kept the endoparasites alive for identification.

The approach for parasite retrieval in connection to Paper II included the task of getting the plerocercoid larvae, otherwise encysted in the viscera of their infected host, to perform excystation. This was done by mimicking the acidic stomach environment of their final hosts by placing the infected tissue in petri dishes filled with artificial digestive fluids. Parasite larvae that had perform excystation were then collected identified and counted.

The technique used to retrieve parasites in Paper III was markedly different. As the process of searching for intestinal parasites is very time consuming, the intestinal track, including pyloric caeca, was frozen down in the field after the protocol analyses of the fish had been done and the needed measurements and samples had been taken. Later, the intestines were checked for parasites. In some cases, the samples had been stored for several years, but without any observable effect on the biological material. The intestinal samples were thawed, cut open and the content, including that of the blind sacks of the pyloric caeca, were transferred to a glass vial with some water. The vial was shaken vigorously to separate the parasites from the intestinal content after which it was sieved through a 120 µm mesh size net. The sample was then cleaned under running water and transferred to a Petri dish so that the intestinal parasites could be identified and counted.

Terminology

The terms used in this PhD thesis follow the definitions of Bush et al. (1997). Mean abundance is the total number of individuals of a parasite taxon counted in a group of hosts divided by the total number of examined hosts in that group including non-infected individuals. Mean intensity is the total number of individuals of a parasite taxon counted in a group of hosts divided by the total number of infected hosts in that group. Prevalence is the number of hosts in a group infected with a particular parasite taxon divided by the total number of hosts examined in that group. Infrapopulation is used to define all individuals of a parasite taxon found in a single fish host. Infracommunity is used for all individuals of all parasite taxa found in a single fish host. Component population refers to all individuals of one parasite taxon found in all fish hosts in one lake. Component community denotes all individuals of all parasite taxa found in all fish hosts in one lake.

Statistical analyses

Some advanced statistical methods were used in the data analyses connected to this PhD thesis and could benefit from some additional clarification.

As part of the data analyses performed in Paper I, a non-metric multidimensional scaling (NMDS) ordination method was applied. The analysis was done to illustrate the structural similarity between infracommunities in the two stickleback populations. The NMDS is based on the Bray Curtis dissimilarity index that gives high weight to more abundant species and is calculated on original abundances. However by log+1 transforming the parasite abundance data the analysis was directed towards a more species compositional approach. Bray Curtis dissimilarity index calculates the relative similarity between all infracommunities based on their parasite abundance and composition. These similarities, expressed as distances (short distance = high similarity, long distance = low similarity), are then put in multidimensional space so that the similarity between infracommunities are matched in the best way possible. The NMDS is then created by projecting this down onto a two dimensional surface making it possible for us to visually interpret the outcome. How well the NMDS restored the calculated Bray-Curtis dissimilarities between the infracommunities is estimated with a stress function that ranges from 0 to 1. Values close to 0 indicate a good fit (Krebs 1999; Greenacre and Primicerio 2014).

For the data analyses of Paper II, a zero-altered negative binomial (ZANB) modelling approach was used. Typically for parasite count data, many hosts are found not to be infected and are thus assigned a zero value. In addition to the commonly overdispersed distribution of most parasite species, parasite count data is therefore typically what is called zero-inflated and highly skewed. Following the directions of Zuur et al. (2009), we turned to advanced modelling in order to account for this extreme data distribution encountered in Paper II. Parasite count

data can contain both false and true zeroes sensu Martin et al. (2005), but we chose to model the data treating zeroes as just zeroes as our overall questions were concerned with whether the fish were infected or not, and if so, how infected.

In Paper 3, a correspondence analysis (CA) was implemented in order to study compositional differences in infracommunities between sampling years. The CA is a widely used ordination method within ecology as it is particularly applicable to count data such as parasite abundances. The method assigns weights to infrapopulations relative to their respective infracommunity. Differences between infracommunities are then transformed to a chi-square distance that gives higher weights to infracommunities with high abundances of parasites. Square root data transformation was however used to reduce this feature and to give a more informative plot. The CA orientates all infracommunities in multidimensional space relative to each other based on their respective chi-square distances. The plot is then made readable in 2D by using the two dimensions that explains the largest amount of total inertia in the dataset as axes, so that multivariate structural tendencies in the data can be observed (Greenacre and Primicerio 2014).

To analyze how parasite abundance varied with environmental variables, a canonical correspondence analysis (CCA) was used. The CCA is similar to the CA, but instead of projecting the differences between infracommunities in an unconstrained space, the CCA projects the data into a constrained space where the dimensions are linear functions of the environmental variables (Greenacre and Primicerio 2014).

For descriptions of additional materials, terms and statistical methods used in the data sampling and analyses of the material that makes up the basis of this PhD thesis, the reader is referred to the respective papers.

Summary of papers

Paper I

Parasite communities of two three-spined stickleback populations in subarctic Norway — effects of a small spatial-scale host introduction

Background

Three-spined sticklebacks in Lake Takvatn were originally introduced from the nearby Lake Sagelvatn. By analyzing the parasite communities of these two populations, we studied the compositional difference in parasite communities at a small spatial scale and the potential introduction of parasite species following the introduction of a new host species.

Hypotheses

1. At the component community level, the metazoan parasite communities of the two three-spined stickleback populations would be generally similar.
2. Inter-lake differences in parasite species composition would be caused by autogenic parasites.
3. The parasite community in the introduced three-spined stickleback population would be less species rich than in the source population.
4. The highest total number of parasites would be found in the lake with the highest density of three-spined sticklebacks.

Results

All sampled sticklebacks were highly infected, particularly with eye-infecting metacercariae. Twelve parasite taxa were recorded, including seven cestodes (*Eubothrium* spp., *Cyathocephalus truncatus*, *Schistocephalus solidus*, *Diphyllbothrium* spp., *D. dendriticum*, *D. ditremum*, *Proteocephalus* sp.), one nematode (Nematoda spp.), one monogenean (*Gyrodactylus arcuatus*) and three digeneans (*Crepidostomum* spp., *Apatemon* sp., *Diplostomum* spp.). Most of these parasite taxa transmit trophically to their fish host through infected copepods. The three taxa, *G. arcuatus*, *Apatemon* sp. and *Diplostomum* spp., are however directly transmitted by free-living parasite stages. In addition, *G. arcuatus*, *S. solidus* and *Proteocephalus* sp. are considered stickleback specialists.

The parasite component communities in the two stickleback populations were very similar and showed high percentage similarity. All identified parasite taxa from the source stickleback population, of which most were allogenic, occurred in the introduced population with overall similar abundances, mean intensities and prevalences. Inter-lake differences in parasite community composition were instead driven by autogenic parasite taxa. At the infracommunity level, a NMDS plot also indicated substantial degree of overlap between the two parasite populations.

At the infrapopulation level, parasite intensity was however higher in the source population for the two autogenic stickleback specialists *G. arcuatus* and *Proteocephalus* sp. whereas no difference was found for the allogenic diphylobothrid cestodes. Overall, quantitative dissimilarities between the two parasite communities were as expected, caused by inter-lake differences in stickleback and intermediate host density.

Nine of the 12 identified parasite taxa occurred in both lakes whereas three (*Eubothrium* spp., *Crepidostomum* spp. and Nematoda spp.) only occurred in the introduced stickleback population. These parasite taxa were however uncommon or normally infect sympatric salmonids.

The highest relative stickleback density and total number of parasite individuals occurred in the source population.

Conclusions

1. High similarity between the two parasite component communities was assumedly caused by the close geographical distance between the two lakes causing high ecosystem similarity and a shared parasite species pool. All parasite taxa including autogenic stickleback specialists appeared to be successfully transferred and established in the introduced stickleback population. None of them “missed the boat” or “drowned on arrival”, *sensu* MacLeod et al. (2010).
2. Autogenic parasite taxa caused inter-lake differences in parasite community composition while the allogenic ones had similar abundances in both stickleback populations presumably caused by their superior dispersal capabilities. The allogenic *Diphylobothrium* spp. did account for most of the dissimilarity between infracommunities between the two populations possibly connected to inter-lake differences in intermediate host density (copepods).
3. The contradicting lower total number of parasite taxa in the source stickleback population was explained by successful transferring and establishment of autogenic stickleback specialists and accidental infections of salmonid parasite species in the introduced stickleback population, illustrating the importance of sympatric fish.
4. The lake with highest density of sticklebacks also had the highest total number of parasite individuals indicating the significance of host density.

Summary of papers

Paper II

Effects of fish species composition on *Diphyllbothrium* spp. infections in subarctic brown trout - is three-spined stickleback a key species?

Background

A comparative study of eight lakes in northern Norway, including brown trout in allopatry (Group 1), trout in sympatry with Arctic charr (Group 2) and trout in sympatry with three-spined stickleback, with or without charr present (Group 3), allowed for the possibility to analyze how the availability of fish prey might affect the *Diphyllbothrium* spp. infections in brown trout.

Hypotheses

1. *Diphyllbothrium* spp. infections in trout would vary among the three groups of fish species composition.
2. Trout in Group 1 would show low infections of *Diphyllbothrium* spp.
3. Trout in Group 2 would show intermediate infections of *Diphyllbothrium* spp.
4. Trout in Group 3 would show high *Diphyllbothrium* spp. infections.
5. *Diphyllbothrium* spp. infections in trout from all groups would increase in intensity as a function of fish size due to the accumulation of parasite larvae in the fish host.

Results

Overall, *Diphyllbothrium* spp. infections in trout differed between the three groups. Mean abundance, prevalence and mean intensity was significantly higher in Group 3 and Group 2 compared to Group 1, whereas Group 3 was significantly higher than Group 2 with respect to mean abundance and mean intensity, but not concerning prevalence.

According to the ZANB model, trout body length significantly explained the probability of *Diphyllbothrium* spp. infection. A 50 % probability of *Diphyllbothrium* spp. infection was indicated in trout 35 cm in length when living in allopatry, 19 cm in length when living in sympatry with charr, and 22 cm when living in sympatry with stickleback, with or without charr present. Fish species composition also explained the probability of infection. Trout in Group 1 had lower probability of infection compared to trout in Group 2 and Group 3, whereas trout in Group 2 and Group 3 differed only slightly.

The ZANB model also identified an interaction between trout length and fish species composition as a significant explanatory variable in predicting the intensity of *Diphyllbothrium* spp. infection. Predicted intensity of *Diphyllbothrium* spp. for trout in Group 1, was thus low for all sampled fish lengths and was always less than one. In comparison, intensity of *Diphyllbothrium* spp. in trout from Group 2 and Group 3 increased

distinctly with trout length, in particular for trout from Group 3. For trout > 40 cm, the intensity of *Diphyllbothrium* spp. was predicted to be 10 times higher in Group 3 than in Group 2. In fact, the largest and most heavily infected brown trout individuals were found in Group 3, presumably as a result of the availability of sticklebacks as prey.

Conclusion

1. *Diphyllbothrium* spp. infections were overall significantly different in the three groups of trout presumably because of the between-group differences in the availability of potential fish prey.
2. Allopatric trout had a low rate of infection, likely caused by the absence of fish prey. They did however show some infection, presumably caused by infrequent copepod predation.
3. Trout in sympatry with charr were intermediately infected, probably caused by charr being a relatively difficult prey to catch, with relatively low parasite infection.
4. Trout in sympatry with stickleback, with or without charr present, had overall the highest infections. Presumably, this was caused by the availability of the relatively easily caught and highly infected stickleback as prey.
5. Significant increase in parasite intensity with trout length from all three groups, were interpreted as confirmation of the accumulating tendency of *Diphyllbothrium* spp.

Summary of papers

Paper III

Temporal changes and structural variation in the intestinal parasite community of Arctic charr in a subarctic lake

Background

The fish community in subarctic Lake Takvatn has been sampled in consecutive years over the past two decades to document changes in the fish population following a mass removal of Arctic charr in the 1980s (Klemetsen et al. 2002). This made it possible to analyze potential temporal changes and structural differences in the intestinal parasite infracommunities of Arctic charr by processing material from 1995 and consecutive years from 2001-2007, 2010 and 2014.

Hypotheses

1. Environmental changes following the mass removal of charr in Lake Takvatn caused variation in the exposure of Arctic charr to trophically transmitted parasites, causing long-term temporal variations in intestinal parasite infracommunity composition.
2. Dietary specialization of Arctic charr would result in heterogeneity in intestinal parasite composition giving rise to spatial variability between hosts.
3. Intestinal parasites, which utilize the same microhabitat, would show reduced occurrences when potential competing species with high intensities co-existed in the same microhabitat.

Results

Throughout the years *Eubothrium salvelini* and *Crepidostomum* spp. occurred overall as core species (*sensu* Hanski 1982), with high mean intensity and prevalence. In some years, nearly all sampled fish were infected. Intensity of both parasite taxa varied significantly with 'sampling year'. *Proteocephalus* sp. and *Cyathocephalus truncatus* appeared as satellite species (*sensu* Hanski 1982), with low mean intensity and prevalence. Only intensity of *Proteocephalus* sp. varied significantly with 'sampling year'.

Co-infection with *E. salvelini* and *Crepidostomum* spp. were the most frequently occurring parasite composition, followed by infracommunities with only *E. salvelini*. Infracommunities with all four taxa present at the same time occurred in only one fish and was the only time where *Proteocephalus* sp. and *C. truncatus* co-existed.

The mean intensity of *E. salvelini* did not differ between infracommunities in which *E. salvelini* was the only cestode species present compared to infracommunities where *Proteocephalus* sp. or *C. truncatus* co-occurred.

Average infracommunity composition separated significantly among certain years according to the second dimension of the CA. Generally, average infracommunities high on *E. salvelini* separated from those high on *C. truncatus* and *Crepidostomum* spp. In addition, the CCA identified 'sampling year' as a significant explanatory variable to explain the variation in the parasite abundance data.

Overall, despite some sporadic temporal variation, no long-term temporal changes or cyclic tendencies were observed in any of the analyses.

Conclusion

1. Sporadic temporal variation in average infracommunity composition was observed and appeared to be connected to changes in infracommunities more abundant on *E. salvelini*, towards infracommunities more abundant on parasite taxa residing in the littoral zone. Presumably, this was associated with possible changes in intermediate host density or habitat utilization by charr. However, overall, long-term temporal stability among years indicated that the system might be in steady state. Possible temporal effects on the intestinal parasite infracommunities of Arctic charr, indirectly caused by the fish removal in the 1980s, therefore seems to be no more.
2. Spatial variation was identified between infracommunities as the parasite species composition varied between individual hosts. Overall stability was however present as co-infection with *E. salvelini* and *Crepidostomum* spp. was the most frequent. Despite individual diet specializations in Arctic charr, the majority of hosts in Lake Takvatn still seemed to be feeding on the two major prey items of the lake.
3. No inter-specific competition in the form of a crowding effect caused by *E. salvelini* was observed between the cestode taxa, indicating that the intestinal parasite community of Arctic charr might be of an isolationistic nature. However, the absence of co-infection with *Proteocephalus* sp. and *Cyathocephalus truncatus* might be an indication of such but could also be caused by strong habitat segregation of the two parasite taxa.

Discussion

The work connected to this PhD thesis discovered generally high similarity, predictability and stability of various parasite communities in freshwater fish from northern Norway, both in time and space. Possible changes to the recipient environment following a small spatial scale introduction of a host species and its associated parasite were elucidated along with the importance of fish prey for the parasite community of a piscivorous fish population.

High similarity was identified between the parasite community of an introduced stickleback population and that of the nearby source stickleback population indicating that there is a high chance of introducing parasites along with a host introduction on a small spatial scale. Marked changes to the original food-web of the recipient ecosystem can also be expected directly as a cause of the introduction of a new host species, but indirectly also through introduced parasite species with potentially large disruptive effects. The work additionally documented high predictability in the infections of a trophically transmitted parasite genus, as its infections of a piscivorous fish population was directly dependent on the presence of sympatric fish species. Especially three-spined stickleback caused increased levels of infections, emphasizing again the potential ecological impact of translocating this fish species. Finally the work discovered high degree of temporal and spatial stability in the intestinal infracommunity of Arctic charr, in addition to identifying it as an isolationistic community with low interaction among parasite species.

Parasite community similarity

The majority of publications dealing with host introduction are concerned with what effects are present on a large spatial scale (Poulin and Mouillot 2003; Kelly et al. 2009; Vignon et al. 2009; Lymbery et al. 2010; Roche et al. 2010; Gendron et al. 2012). From such studies, the so called 'enemy release' hypothesis might be observed which indicates that the introduced host is liberated of the parasite burden it faced in the source environment and thus have a competitive advantage in the recipient environment (Torchin et al. 2002; Torchin et al. 2003; Vignon et al. 2009; Roche et al. 2010). Parasite communities are under regulation by several different abiotic and biotic factors in both space and time (Holmes 1987; Holmes 1990). Geographical distance-induced changes in such abiotic and biotic factors are therefore likely the cause of 'enemy release' (Poulin 2007; Kennedy 2009; Karvonen et al. 2013) and presumably also contributing to the widely observed tendency for parasite community similarity to decrease with increasing geographical distance (Poulin and Morand 1999; Poulin 2003; Perez-del-Olmo et al. 2009; Locke et al. 2012).

In contrary to decreased similarity, the present study found that the parasite community of the introduced stickleback population in Takvatn was highly similar to that of the source stickleback population in Sagelvatn on a small spatial scale. These results thus indicate that when host introduction is performed on a small spatial scale, successful transmission and colonization of essentially all parasite species of the original host population are likely to take place in the introduced environment causing high similarity between local parasite communities (Paper I). Similar biotic and abiotic factors were presumably part of the reason for this high similarity between local parasite communities. To generalize, parasite communities might be overall similar on a small spatial scale if the environments in question are similar with regards to the abiotic and biotic factors important for the successful introduction and establishment of parasites.

Parasites introduced along with a host introduction

The results of this study suggest great degree of successful introduction and establishment of parasite species when host introduction is done on a small spatial scale (Paper I), with a low probability of parasite taxa to 'miss the boat' or 'drown on arrival' (*sensu* MacLeod et al. 2010). Between environments with similar biotic and abiotic conditions, separated by a short geographical distance, allogetic parasite taxa have great dispersal and colonization capabilities indicated by similar mean intensity and prevalence (Paper I) which is in line with the relatively high dispersal abilities associated with this life cycle strategy (Fellis and Esch 2005). Avian final hosts are presumably distributing eggs of allogetic parasite species between such environments contributing to the high similarity observed between parasite communities on a small spatial scale (Paper I). Allogetic generalists have likely already colonized the recipient environment prior to host introduction as they might have the opportunity to infect fish species already present in the recipient environment (Bush and Kennedy 1994; Poulin and Morand 2004). On the other hand, allogetic parasite species specialized on the specific species of the introduced host, will be directly dependent on that host colonizing the recipient environment in order for themselves to successfully colonize the recipient environment. Allogetic specialists are likely introduced prior to host introduction by their avian final hosts, but need their specific host to complete their lifecycle. Regarding autogenic parasite taxa, these are likely completely dependent on host introduction in order to be distributed to other environments as they have their adult and final stage in the fish host. The effect of anthropogenic host introduction with regards to the introduction of parasite species can thus be viewed as more disruptive when it comes to autogenic parasites and specialized parasites, as allogetic parasite presumably are naturally dispersed between environments on a small spatial scale. Host introduction on a small spatial scale thus reflects a variety of potential introduction pathways with both autogenic and allogetic parasites possibly being introduced along with the host introduction, independent dispersal of allogetic parasites by avian hosts from the source environment or

other sources, and those already infecting established fish populations in the recipient ecosystem prior to host introduction. In the present study, parasite taxa that contributed most to the parasite community dissimilarity between lakes were copepod transmitted allogenic cestodes and autogenic stickleback specialists, emphasizing that the life-cycle strategy of a parasite species is still important for successful colonization, also on a small spatial scale.

Ecological changes following host introduction

Host introduction, especially in the case of three-spined stickleback, can potentially alter the topology of the food web of a recipient lake (Amundsen et al. 2013). Several changes are thought to have come along with the introduction of three-spined stickleback to Takvatn. Possibly the most significant are how three-spined stickleback might function as prey, and how it might facilitate parasite transmissions in the food web of the recipient lake. In Takvatn, the presence of three-spined stickleback has presented an additional highly attractive prey item for brown trout and Arctic charr, but also for several bird species of which the colonization of some are believed to be a direct cause of the presence of three-spined stickleback (Amundsen et al. 2013). The degree of which birds forage, and therefore emits parasite eggs into a lake system, presumably increases when an easy caught prey such as three-spined stickleback is introduced (Whoriskey and Fitzgerald 1985; Reimchen 1990; Amundsen et al. 2013). The occurrence of trophically transmitted parasite species that use zooplankton as intermediate host, are likely also intensified as three-spined stickleback can be a heavy zooplankton feeder, thus amplifying the rate of successful host infection for parasite species utilizing this intermediate host (Jørgensen and Klemetsen 1995; Langeland and Nøst 1995). As three-spined stickleback in Takvatn appears to be highly infected with a diverse parasite community (Paper I) and at the same time function as prey of salmonids and birds, they are important in the facilitation of trophically transmitted parasite species through the food web. Of special importance is the transmission of plerocercoid larvae of the cestode genus *Diphyllbothrium* and the allogenic three-spined stickleback specialist *Schistocephalus solidus*. Among the parasites introduced to Takvatn along with the three-spined stickleback introduction (Paper I), *S. solidus* is presumably one of the parasite species with potentially largest effect on the food web and ecology of Takvatn. The reason is that *S. solidus* is capable of severe host manipulation increasing the predation rate of infected three-spined sticklebacks by both fish and birds (Moore 2002; Barber 2013 and references therein). This likely increases the transmission rate of *S. solidus*, but also other trophically transmitted parasites such as *Diphyllbothrium* spp. In Takvatn, 25 % of the sampled stickleback analyzed in the present study were infected with *S. solidus* indicating the potential ecological significance of this parasite species (Paper I).

The significant effects that the three-spined stickleback and associated parasites have had on the food web structure in Lake Takvatn is again an indication that host introduction, with

regards to introduced parasites, possibly is more disruptive on a small spatial scale compared to a large spatial scale. On a small spatial scale, parasites with potential large ecological effects are presumably more likely to successfully colonize the recipient environment. While the main concern regarding host introduction performed on a large geographical scale is the potential impact the host itself will have on the recipient ecosystem, parasite introduction should according to the present study be an additional concern when hosts are introduced on a small spatial scale.

The importance of sympatric fish species

As a trophically transmitted parasite genus, *Diphyllobothrium* is largely dependent on the second intermediate host (fish) preying on the infected first intermediate host (copepods). In Norwegian brown trout populations, copepod feeding is not considered to be a common dietary choice, but can be observed in minor degree from allopatric populations (Langeland et al. 1991; Knudsen et al. 2008; Jonsson and Jonsson 2011; Eloranta et al. 2013; Sánchez-Hernández and Amundsen 2015; Paper II). Even in the absence of prey fish, brown trout is thus still, but to a minor degree, exposed to infections by *Diphyllobothrium* spp. through infrequent copepod feeding (Paper II). The transmission route available for *Diphyllobothrium* spp. in allopatric trout populations therefore appears to be inefficient in completing the life cycle of this parasite taxa (Paper II). However, when a fish host such as three-spined stickleback, which feeds commonly on copepods and are possible prey for brown trout, are introduced to an allopatric trout population, the transmission scheme of the parasite taxa is changed as new transmission routes become available. Norwegian brown trout populations are not observed to have cannibalistic tendencies as small and large sized brown trout utilizes different habitats (L'Abée-Lund et al. 1992; Klemetsen et al. 2003; Knudsen et al. 2008; Sánchez-Hernández and Amundsen 2015). However, when in sympatry with three-spined stickleback or Arctic charr, brown trout has the opportunity to turn piscivorous. Lacustrine salmonids starts to include fish prey in their diet at about 15 cm in length, but the trait can be observed in fish of a smaller size if three-spined stickleback is available as prey (L'Abée-Lund et al. 1992; Keeley and Grant 2001; Eloranta et al. 2013). According to the results of this study, it appears that the tendency of brown trout to turn piscivorous is not affected by whether three-spined stickleback or Arctic charr is available as prey (Paper II). The frequency of fish predations seemed however to differ as the infections of *Diphyllobothrium* spp. in brown trout with the possibility to prey on three-spined stickleback, were higher compared to brown trout that only had the possibility to prey on Arctic charr (PAPER II). It is likely that parasites capable of re-infecting piscivorous fish, such as *Diphyllobothrium* spp. (Hammar 2000; Gallagher and Dick 2010), increase their transmission rate to the second intermediate host as a transmission link through piscivory becomes available when a potential fish prey is introduced to a recipient lake (Paper II). However, in Takvatn, piscivory is more common in large-sized brown trout, which might function as dead

end hosts for *Diphyllbothrium* spp. as their size liberate them from predation by birds, thus disrupting *Diphyllbothrium* spp. in reaching its final host.

Fish species composition can influence predator-prey interactions, habitat choice and feeding behavior of a fish species, all of which are important factors in structuring the parasite community of a fish population (Wootton 1998; Knudsen et al. 2004; Knudsen et al. 2008; Fernández et al. 2010; Paper II). Lakes that vary in species composition are therefore also likely to vary in the occurrence of trophically transmitted parasites such as *Diphyllbothrium* spp.

At high intensities, *Diphyllbothrium* spp. might cause mortality in their salmonid hosts and can potentially lead to human infections, which stresses the importance of managing freshwater fish populations carefully (Henricson 1977; Rahkonen et al. 1996; Hammar 2000; Wicht et al. 2008; Kuchta et al. 2013). Concerning recreational fishing and fish population management, introducing three-spined stickleback could be considered beneficial as it likely increases the overall size of the brown trout in the recipient environment by presenting a lucrative prey item. In contrary, however, anthropogenic fish translocation might want to be discouraged of in order to keep the *Diphyllbothrium* spp. infections in the environment at a low level.

Spatial and temporal variation

By heavily reducing the fish density of an overcrowded fish population, it is possible to bring along changes to the fish community such as dietary shifts following within population change in e.g. habitat utilization (Amundsen and Kristoffersen 1990; Klemetsen and Dahl-Hansen 1995; Persson et al. 2007). Changes such as these are likely to affect to what extent a host is exposed to trophically transmitted parasite species as the infections of such parasites are linked to the feeding behavior of the host (Klimpel et al. 2003; Knudsen et al. 2004; Valtonen et al. 2010; Locke et al. 2014). The intestinal parasite infracommunity can therefore be seen as a good indicator of the dietary choice of the fish.

From the present study, high infection levels in Arctic charr were found among the intestinal parasite species that use the preferred prey item of this fish host as intermediate hosts.

Habitat utilization and seasonality of the intermediate host as well as longevity in the final fish host were presumably important for determining whether parasites occurred as 'core' species or 'satellite' species, *sensu* Hanski (1982) (Paper III).

To what degree a parasite community of a recipient environment is affected by a perturbation, such as an introduction of a host species and associated parasites might be dependent on what level of variation is already present within the parasite community.

Helminth endoparasite communities of freshwater fish are considered inherently unstable,

as no regulating factors have been identified (Kennedy 1977; Kennedy and Rumpus 1977; Kennedy 2009). General observed stability is likely caused by environmentally stable biotic and abiotic factors (Kennedy 1977; Kennedy and Rumpus 1977; Kennedy 2009). A seemingly stable but unregulated parasite community would likely experience changes following a perturbation such as the introduction of a new host species and associated parasites. Overall, spatial stability in the intestinal infracommunities of Arctic charr in Lake Takvatn was present as a few specific infracommunity structures dominated (Paper III). This indicated favorable transmission of certain taxa, regardless of the tendency for feeding specialization seen in charr.

Sporadic temporal variation in the intestinal parasite infracommunity of Arctic charr was observed in the present study, presumably caused by a dietary switch from a copepod-dominated diet to a more benthic crustacean dominated diet (Paper III). These changes were expected to have been brought along by changes in environmental factors such as the occurrence of intermediate hosts, fish density and habitat utilization by Arctic charr (Amundsen and Kristoffersen 1990; Dahl-Hansen 1995; Klemetsen and Dahl-Hansen 1995; Persson et al. 2007). Overall temporal stability in the average composition of intestinal parasite infracommunities in Arctic charr from Takvatn was however the result of this study (Paper III), indicating an overall temporally stable average feeding behavior of Arctic charr which is in contrast to the general belief of strong dietary specialization in charr (Knudsen et al. 2011). The results do not exclude dietary specialization, but instead indicate that the main prey items available in the habitat are still utilized to some degree by Arctic charr regardless of dietary specialization. Long-term stability also indicates that the intestinal parasite assemblages of Arctic charr in Lake Takvatn is in a relative steady state following the extensive Arctic charr removal in the 1980s.

Overall, spatial and temporal stability in the intestinal parasite infracommunity of Arctic charr in Takvatn indicates that a perturbation such as the introduction of a new host species and associated parasites would likely affect the community significantly.

Shortage of space may cause inter-specific competition between parasite species residing in the same microhabitat such as the intestine of Arctic charr (Crompton 1973). However, according to the results of the present study, it appears that no inter-specific competition in the form of a crowding effect was present among intestinal cestode parasites infecting Arctic charr (Paper III). These results are in accordance with other parasitological studies performed on salmonids (Halvorsen and MacDonald 1972; Knudsen et al. 2008). Generally, the intestinal helminth community of freshwater fish are considered isolationistic in nature as interactions between parasites are rarely seen, indicating that pre-transmission factors, such as density of potential intermediate hosts and host feeding behavior, are likely the most important for the structuring of the intestinal parasite community of freshwater fish (Kennedy 1990; Paper III). Introduced parasite species would presumably establish more easily in a host where the co-existing parasite community is of an isolationistic nature and thus aiding in successful colonization of the recipient environment.

Conclusion

The present study revealed high similarity, predictability and stability in parasite communities of freshwater fish from Northern Norway.

High similarity was documented between the parasite community of an introduced and a nearby source three-spined stickleback population, indicating high chance of introducing parasites along with a host introducing on a small spatial scale. Marked changes to the recipient ecosystem was observed following host introduction. Three-spined stickleback functioned as prey for other fish species, and likely facilitated the transmission of several trophically transmitted parasite species in the recipient food-web. The co-introduced parasite species also had potential ecological disruptive effects. Especially the introduction of autogenic parasites and specialized parasites were of importance and directly connected to this host introduction. Main concerns regarding host introduction performed on a large geographical scale seem to be the potential impact the host itself has on the recipient ecosystem. However, according to the results of this study, parasite introduction should be an additional concern when host introduction is performed on a small spatial scale.

High predictability was documented in the infections of a trophically transmitted parasite genus as the infection levels of a piscivorous fish population was directly dependent on the presence of sympatric fish species. By introducing a host species feeding commonly on the intermediate host of a parasite species capable of transmitting from prey fish to fish predator, the transmission scheme of the parasite is changed as new transmission routes become available causing significant changes to the food-web and the overall ecology of the recipient environment.

High stability both temporally and spatially was documented in the intestinal parasite infracommunity of Arctic charr indicating that a perturbation such as the introduction of a new host species and associated parasites could potentially bring along significant changes to the parasite community. In addition, as the parasite infracommunity of Arctic charr was found to be isolationistic of nature, newly introduced parasites with the potential to infect Arctic charr would presumably establish more easily in this microhabitat leading to a higher chance of successful colonization.

Anthropogenic host introduction is a common practice taking place both globally and locally (Kolar and Lodge 2002; Garcia-Berthou et al. 2005). According to the result of this study, it is strongly advised to discourage this practice especially on a small spatial scale, as local host introduction is likely to bring along not only environmental changes induced by the introduced host, but also significant changes in the food-web topology and ecology of the recipient environment caused by introduced parasite species.

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