

Parasite communities of two three-spined stickleback (*Gasterosteus aculeatus*) populations - Effects of a local-scale host introduction?



Jonas Jakobsen

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SUMMARY

The introduction of new hosts into new habitats can bring along hitchhiking parasites, i.e. parasites being introduced with the host. This in particular can be an important dispersal mechanism for autogenic parasites that are otherwise restricted by the natural movement of their fish hosts.

In this study, the effect of a local introduction of three-spined sticklebacks (*Gasterosteus aculeatus*) was examined by comparing the macroparasite communities of the introduced and founder population in two subarctic lakes. Seasonal variation and inter-lake difference in abundance was also described, and integrated in the analysis. 120 three-spined sticklebacks were sampled in each lake during three sampling periods in June, August and October 2010. With the exception of the few rare parasite taxa, the parasite communities in the two lakes were highly similar. A total of 14 macroparasite species or taxa were recovered from the sticklebacks, including eight cestodes, one monogenean, one nematode and four digeneans. The parasite communities were dominated by generalist parasite taxa and with an equal number being auto- and allogenic. Ten of these parasite taxa were present in both populations, while four was not. As expected, due to limited dispersal abilities, the non-shared parasite taxa were all autogenic. None of these however, were stickleback specialists, but generalists or specialists infecting sympatric salmonids and showed low infections in the sticklebacks. A gyrodactylid monogenean and a proteocephalan cestode were the only autogenic stickleback specialists and were, as they were present in both populations, assumed to have been introduced with the stickleback.

Cestode and digenean larvae were the most abundant parasites in the sticklebacks in both lakes, with diplostomid metacercaria being by far the most numerous. Other abundant parasite groups were diphyllbothrids and encysted metacercaria. Inter-lake differences in abundance were highest between the two introduced stickleback specialists, as they were more abundant in the founder population. In general, abundances were higher in the founder population, and likely a reflection of higher fish host densities. Many of the parasites exhibited seasonal variation in abundance with peak levels in August and lower levels in June and October, reflecting an increase in new infections during early summer, and reduction due to mortality of the oldest and most heavily infected sticklebacks in late summer.

The present study suggests that many of the mechanisms otherwise influencing parasite communities are of lesser importance on a local scale due ecosystems being highly similar. Accordingly it shows that local scale fish introductions are more likely to bring along hitchhiking parasites, than introductions on a larger geographical scale.

Front cover picture: One of the sampled three-spined sticklebacks infected with two plerocercoid larvae of the cestode *Schistocephalus solidus*.

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1. INTRODUCTION

Host introductions may have important consequences for both the native free-living community of organisms and on the structure of parasite communities of the involved host species (Williamson 1996). Fish have been introduced on global and local scales, both deliberately and accidentally (Kolar and Lodge 2002; Garcia-Berthou *et al.* 2005) and, as many fish species harbour numerous parasite species, these can inevitably and unknowingly be introduced as hitchhikers (i.e. parasites being introduced with the host and colonising the new habitat). Some of these introduced parasites may have devastating effects on native host populations or ecosystems (Daszak *et al.* 2000; Cleaveland *et al.* 2002). Though many studies have focused on the introduction of exotic species (Poulin and Mouillot 2003; Kelly *et al.* 2009; LyMBERY *et al.* 2010; Roche *et al.* 2010), few have addressed the effects of local-scale introductions of native fish species. A successful introduction of new parasite species is dependant on a number of factors allowing for dispersal and colonisation. These factors of both abiotic and biotic character are important in structuring parasite communities (Poulin 2007; Kennedy 2009) and can be expected to lead to greater similarity on a local scale. In the present study, the effects of a local-scale host introduction were examined in three-spined stickleback (*Gasterosteus aculeatus*). The parasite communities of this host species were compared between a founder and an introduced population in two lakes in subarctic northern Norway.

Parasites of freshwater fish represent a well studied area within parasitology, and study systems are often well defined and it is simple to obtain sufficiently large sample sizes. Previous studies have sought to identify patterns of variation in parasite communities (Poulin 2007; Kennedy 2009), and describe the different factors determining the abundance and distribution of freshwater fish parasites. In ecological parasitology, parasites are defined in space and time and classified at different levels according to the unit of study. At the highest level, the supra-community includes all species of parasites in all their hosts, as well as all free-living stages. The component-community includes all species of parasites in one host species population. Lastly, the infra-community refers to all species of parasites in one single host individual. A parallel level of classification is applied to parasite populations, but then just referring to a single parasite species (Bush *et al.* 1997). In the present study, parasite communities were compared on component- and infra-community levels, as well as on a component-population level.

Individual parasite species are classified further with regard to dispersal modes and host specificity. The mode of dispersal of parasites of freshwater fishes is termed autogenic when the lifecycle is completed within a water body and fish are final hosts, and allogenic when the parasite exploit mammalian or avian final hosts and thus have part of its lifecycle outside a water body (Esch *et al.* 1988). Autogenic parasites have therefore limited dispersal abilities compared to allogenic parasites in which avian or mammalian hosts can disperse parasite eggs over large distances. Host specificity varies between individual species, and parasites can be classified as either being a generalist or specialist. Specialists infect only a single host species, while generalists are capable of infecting a larger range of host species. However, host specificity is usually defined with respect to a specific stage in a parasites lifecycle, as a parasite can be a specialist in one stage and a generalist in the next. For example, the characteristic stickleback cestode, *Schistocephalus solidus* (see front cover picture) is a specialist in the stickleback intermediate host, but a generalist in the adult stage where it infects a large range of piscivorous birds (Hoffman 1999).

A parasite species is dependent on both successful dispersal and colonisation to be found in a given host population. Dispersal enables a parasite to reach a given habitat and colonisation is the establishment of new infections in that habitat. The success of both dispersal and colonisation depends on whether a range of conditions are met or not. Holmes (1987, 1990) defined a series of different filters, or factors that determines the structure of parasite communities leading from dispersal to colonisation. The parasites that are geographically available to infect a given host population is determined by biogeography and can also be affected by host introductions. Thereafter, the environmental factors in the habitat of both an abiotic and biotic character must allow for colonisation of a given parasite species. As many parasite species have complex lifecycles as well as free living stages, they are often dependent on specific environmental conditions and the presence of several different host species. Therefore, if a parasite species is regionally available in the species pool, and the biotic and abiotic demands are met within the habitat, the parasite will be present in the local parasite community. Secondly, a range of factors working both at the population and individual level of the hosts further affect the structure of the parasite community. These factors are of ecological, physiological and phylogenetic characters and include host behaviour and physiology as well as phylogenetics, specificity and even interactions among parasites. All these factors lead from the local parasite fauna available to the establishment of a realised component-community and the different infra-communities within a host population.

Biogeography has been well studied for different fish parasites (Marcogliese 1992; Morand and Krasnov 2010; Poulin *et al.* 2011b). As parasites are inextricably linked to and dependent on its host, the geographical range of suitable hosts sets the boundaries for a parasite species' expansion range, and, also link parasite diversity closely to host diversity (Krasnov *et al.* 2004; Thieltges *et al.* 2011). The biogeography of parasites in general has been reviewed by Morand and Krasnov (2010) and Poulin *et al.* (2011b), for fish by Carney and Dick (2000), and specifically related to parasites of the three-spined stickleback by Poulin *et al.* (2011a). Numerous studies have shown that parasite communities differ (increased similarity decay) with increasing geographical distance (Poulin and Morand 1999; Poulin 2003; Pérez-del-Olmo *et al.* 2009; Thieltges *et al.* 2009). Also host specificity and mode of dispersal have been found to explain geographical similarity decay in parasite communities (Fellis and Esch 2005; Poulin 2010; Poulin *et al.* 2011b). Host specificity affects a parasite's chance to colonize new habitats. Generalists that are able to infect a greater range of hosts are more likely to encounter suitable hosts, and are as such better colonizers and less prone to local extinction. Specialists, on the other hand, are dependent on the presence of specific host species, and thus more likely to become locally extinct (Bush and Kennedy 1994; Poulin and Morand 2004). In addition to natural dispersal, species introductions is one way in which parasite species, otherwise restricted in dispersal, can be introduced to new host populations. Parasite introductions most often occur through introduction of infected intermediate or final host species (Kennedy 1976). Introduced fish species are often found to have depauperate parasite communities, because many of the host parasites are either not brought along with the introduction, or fail to establish in the new habitat, termed "missing the boat" or "drowning on arrival", *sensu* Macleod (2010) (Torchin *et al.* 2002; Torchin *et al.* 2003). Still the number of parasite species infecting introduced hosts has been found to rival that of the initial founder population, but often with a change from specialist to generalist parasite species (Kennedy and Bush 1994). Marcogliese and Cone (1991) also found that differences in parasite species richness were best explained by sympatric fish species, and generally sympatric fish species are found to share many of the same parasites (Baldwin and Goater 2003; Lymbery *et al.* 2010). Despite the importance of sympatric host species and their associated parasites in explaining parasite communities, they are often neglected in such studies (Fernandez *et al.* 2010). Whether new parasite species are introduced with its host or not, a host introduction may also indirectly alter structures in parasite communities through its effect on local ecological interactions (Dunn 2009; Kelly *et al.* 2009).

Following initial dispersal, naturally or by introduction, a parasite must colonise the host population in the new habitat by establishing new infections. Colonisation however, is only possible if requirements for biotic and abiotic factors are fulfilled. Abiotic factors may include e.g. salinity (Poulin *et al.* 2011a) or pH (Marcogliese and Cone 1996), i.e. factors that may directly affect free living stages and ectoparasites. Important biotic factors are, in addition to suitable fish hosts, the presence of required intermediate or final hosts needed for a specific parasite to complete its lifecycle. Abiotic factors may also work indirectly in affecting the presence of intermediate hosts required, as for example pH-levels are correlated with the abundance of molluscs utilised as intermediate hosts by digeneans (Marcogliese and Cone 1996). If a parasite species manage to colonise a new habitat, there are further ecological factors affecting its distribution and abundance within the ecosystem. It is apparent that ecological factors affecting the host species will indirectly have an effect on the parasite species that are dependent on this specific host. Host behaviour, especially with respect to foraging is important in determining parasite communities as there is a direct link between foraging behaviour and the acquisition of trophically transmitted parasites (Knudsen *et al.* 2004; Valtonen *et al.* 2010). However, trophic interactions alone can not explain the infection patterns of trophically transmitted parasites, since host specificity is clearly also a limiting factor (Lagrue *et al.* 2011). Host population dynamics also affects parasite communities, particularly through population density, and generally a positive relationship exists between host population densities and both parasite abundances (Dobson 1990) and species richness (Morand and Poulin 1998; Takemoto *et al.* 2005), acting by increasing transmission rates. Increase in transmission with host density is more important for directly transmitted parasites, while parasites with indirect lifecycles in addition are dependent on the densities of intermediate and or final hosts (Anderson and May 1978).

Numerous parasitological studies have focused on three-spined sticklebacks as they are suitable study objects; they often occur at high population densities, are easy to catch and have a widespread, circumpolar distribution (Wootton 1984). In a review, Barber (2007) sums up a total of 122 macroparasite species recorded from the three-spined stickleback worldwide, including both saltwater, brackish and freshwater habitats. In Norway, a total of 19 macroparasites have been recorded from sticklebacks in freshwater populations (Levsen 1992; Sterud 1999). The local parasite component-communities consist of only a fraction of this due to the aforementioned factors

leading from dispersal to colonisation. In subarctic northern Norway, three-spined sticklebacks were introduced from Sagelvvatn (the suffix *-vatn* = lake) to the nearby Takvatn 60 years ago (Klemetsen *et al.* 2002), altering the food web topology (Amundsen *et al.* 2009) and possibly also introducing hitchhiking parasites (Amundsen *et al.* 2011). In Takvatn, seven species of macroparasites have previously been recorded from the three-spined stickleback (Hope 1992; Amundsen *et al.* 2009). It is likely that the stickleback introduction has brought along hitchhiking parasite species, but how this have affected the parasite communities of the stickleback population and how it can be explained are questions yet to be addressed.

The main objective of the present study was therefore to conduct a comparative analysis of the macroparasite communities of the three-spined stickleback populations in Sagelvvatn and Takvatn, thereby studying the effect of the host introduction and reveal potential differences in parasite species richness and abundance between the founder and the introduced population. Great similarity was expected as the study lakes due to geographical proximity, share the same regional species pool. Similarities should further be enhanced by highly similar ecosystems, and hence similarities in biotic and abiotic factors. Minimising the influence of such factors, allows for a study isolating the mechanisms of parasite dispersal. Allogenic parasite species, being easily dispersed between lakes, are expected to have successfully colonised both stickleback populations. Autogenic parasite species however, being restricted in dispersal, is dependent upon the movement of its fish host to colonize a new habitat. Therefore any eventual differences in parasite species richness are most likely explained by autogenic parasites. Through the introduction of the three-spined stickleback, new hitchhiking parasites could have been able to colonize Takvatn directly with the introduction of their host. However, it is possible that some of these potentially hitchhiking parasite species have been “missing the boat”, *sensu* MacLeod (2010). With respect to abundances of the different parasite species, the general pattern was likewise expected to be similar, but possibly related to differences in environmental factors. Seasonal variation in parasite abundances was also explored, expecting that seasonal variation, likewise due to great similarities, follows the same patterns in both lakes with an increase in abundances through the season due to the accumulation of parasites (Brassard *et al.* 1982; Gaten 1987).

On this background, the following hypotheses with regard to the parasite communities of the founder and introduced stickleback populations were investigated:

- 1) Due to similarity in biotic and abiotic factors, and geographical proximity, the structures of the parasite communities are similar in the two stickleback populations.
- 2) The same allogenic parasite species are present in both lakes, while potential inter-lake differences in species richness are explained by autogenic parasite species.
- 3) The parasite community in the introduced Takvatn population is less species rich than in the founder Sagelvatn population, due to parasites being lost during the host introduction.
- 4) Large differences in host densities between the two lakes will result in differences in parasite abundances, with highest abundances in the lake with highest host densities.
- 5) The seasonal variation in parasite abundances is similar in the two lakes, with an increase through the season due to the accumulation of parasites.

2. MATERIALS AND METHODS

2.1. The study lakes

Sagelvvatn and Takvatn are two oligotrophic, dimictic lakes located in subarctic northern Norway (69°11`N, 19°05`E and 69°07`N, 19°05`E, respectively). The lakes are usually ice covered from November to June, and are located in different catchment areas approximately four kilometres apart. Takvatn is situated 214 m above sea level, has a surface area of 14.2 km² and a maximum depth of ca. 80 m. Sagelvvatn is situated 91 m above sea level, has a surface area of 5.1 km² and a maximum depth of ca. 70 m. The drainage areas are dominated by birch forests and farmland, but Sagelvvatn is surrounded by farmland to a greater extent, and likely subject to slightly higher nutrient inputs from agricultural runoff. Sagelvvatn can be considered as being slightly more productive, reflected by a lower Secchi depth (Sagelvvatn = 8 m, Takvatn=12-14 m) (Primicerio and Klemetsen 1999; Dahl-Hansen *et al.* 2011).

Takvatn and Sagelvvatn support exactly the same fish communities comprised of arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) along with the three-spined stickleback. While Sagelvvatn has experienced a postglacial invasion of all three species, only brown trout was originally present in Takvatn. However, overexploitation of the brown trout led to the introduction of arctic charr from nearby Fjellfroskvatn around 1930 in an attempt to improve the fish catches (Klemetsen *et al.* 2002). Around 1950, three-spined sticklebacks were introduced from Sagelvatnet (Jørgensen and Klemetsen 1995) as an attempt to provide a prey item to boost growth rates within the fish community, now dominated by a stunted arctic charr population. In the 1980'ies, an intensive fishing programme was carried out, and succeeded in decreasing the number of small grown arctic charr, improving growth (Amundsen *et al.* 2007; Persson *et al.* 2007) and reducing parasite loads, especially among copepod transmitted cestodes (R. Knudsen *et al.*, unpublished data).

2.2. Fish collection and parasite screening

120 three-spined sticklebacks were collected from each lake in late June (n=30), mid August (n=60) and mid October (n=30) 2010. Fish were caught with bottom gillnets (mesh sizes 6 – 10 mm) in the

littoral zone at 1 – 8 m depth. In October in Takvatn, and in June in Sagelvvatn, 29 and one fish, respectively, were collected in baited minnow traps as gillnet catches were low. Following capture, each fish was killed by a blow to the head and immediately placed individually in glass jars containing lake water. In the field lab, fish were measured (fork-length to nearest mm) and a complete macroparasite screening was conducted using a stereomicroscope. The skin and fins of each fish was first examined for ectoparasites (ciliates and monogeneans). The different organs and tissues were then dissected and intestine, stomach, eyes, body cavity, liver and swim bladder examined separately for endoparasites.

All macroparasites of each species or taxonomic group were counted. Microparasites (ectoparasitic ciliates) were only noted as present or absent, and not included in the statistical analysis. Species for further taxonomic analysis were preserved in 96% ethanol. Parasite species common to the study systems were classified based on external morphology, based on prior knowledge. Most parasites were determined to genus or species, but others were grouped as follow (see Appendix B for a complete parasite list): The group *Diphyllobothrium* spp. are small (1-5mm), newly established plerocercoids (likely *Diphyllobothrium ditremum* as larger specimens of *Diphyllobothrium dendriticum* were rare). Encysted metacercaria in the eye and body cavity, probably of the genus *Apatemon* as these have been found encysted in the eyes of sticklebacks (Blair 1976), the two might be the same or different species. The proteocephalan cestodes termed *Proteocephalus* sp1. is likely the stickleback specialist *P. filicollis* commonly found in stickleback (Scholz 1999; Scholz *et al.* 2007) although this was not confirmed. *Proteocephalus* sp2. is thought to be a brown trout or arctic charr specialist (*P. exiguous* or *P. neglectus*) (Sterud 1999). The genus *Diplostomum* spp. likely includes both the generalist *D. spathaceum* and the stickleback specialist *D. gasterostei*, but these were quantified to genus only.

2.3. Terms used and statistical analyses

In the statistical analysis and presentation of results, the different species, genus or taxon, under which the different parasites were quantified, are treated as a species and referred to as such. Terms used to describe parasite communities and populations are applied according to the definitions of

Bush *et al.* (1997), and data and results are presented following the recommendations of that paper and Rózsa *et al.* (2000).

Component-community parameters are based on total abundance data, i.e. the total number of each parasite taxa from each population, including all months. As measures of diversity, the component-community species richness (CCR, Norton *et al.* 2003), Simpson index (1/D) and Simpson Evenness measure ($E_{1/D}$) (Magurran 2004) are used. The Simpson index is calculated as:

$$1/D = 1/\sum p_i^2$$

where p is the proportion of species i in the community. It is a diversity index sensitive to changes in the most abundant species and gives lower weight to changes in rare species (Krebs 1999; Magurran 2004). The Simpson evenness is calculated as:

$$E_{1/D} = (1/D)/S$$

where S is the number of species in the sample (CCR). It provides an index (0-1) of how evenly the different parasite species are presented in the component community (Magurran 2004; see also Smith and Wilson 1996). Percentage similarity (or Renkonens Index, Krebs 1999) was used to compare the two parasite component-communities directly and is calculated as:

$$P = \sum(\text{minimum}, p_{1i}, p_{2i})$$

where p_{1i} is the percentage of species i in community 1, and p_{2i} is the percentage of species i in community 2.

Infra-community diversity is based on individual abundance data, each fish being the sample unit. Infra-community species richness (ICR) and number of parasites per fish is used here as measures of diversity. The parasite component-populations are each summarised by prevalence (proportion of hosts infected), mean intensity (mean number of parasites in infected hosts), mean abundance (mean number of parasites in all hosts examined) (Bush *et al.* 1997), and by the variance/mean ratio to provide a measure of dispersion.

A canonical correspondence analysis (CCA) was applied to allow for a multivariate testing of the parasite abundances in the infra-communities as a function of the predictor variables month, population, sex and length. CCA is a direct ordination method, and produce dimensions that are linear combinations of the environmental variables (population, month, sex, length), using the chi-square distance as a distance measure. The CCA is useful for analyzing count data and in particular

zero inflated data (Legendre and Legendre 1998). A CCA was applied to the full data set, and the best CCA model was selected based on the Akaike Information Criterion (AIC).

Nonmetric multidimensional scaling (NMDS), based on Bray-Curtis dissimilarity (Krebs 1999) of log-transformed data, was used to visualize differences in the parasite infra-communities in relation to the population and month variables. The NMDS is a robust, indirect, non-parametric ordination method that is useful for revealing structures of similarities/dissimilarities in various multivariate data (Legendre and Legendre 1998). The Bray-Curtis dissimilarity measure gives higher weight to more abundant species (Krebs 1999), but through log-transforming, the measure is directed towards a more species richness like effect by decreasing the influence of the most abundant species. The NMDS was used here only as an explorative tool to investigate trends and correlations, and no statistical testing or estimation was applied. One NMDS was run and plotted for the full data set to investigate inter-lake variation, and one for each population separately to investigate the seasonal variation. As applied here, the NMDS depict the individual infra-community as relative to all the other infra-communities. The fit of a NMDS is given by the term *stress*, a percentage of how well the actual distance between samples (fish) are represented in the two dimensional bi-plot.

At the component-population level, the individual abundance of each parasite taxa was fitted with a generalised linear model (GLM). Models were fitted with negative binomial errors to account for the large degree of overdispersion exhibited by most of the parasite species (Appendix C). In addition, infra-community species richness (ICR) and total number of parasites per fish were tested with the same models. These modelling efforts were done to adjust for the confounding effects of sex and length. Individual model selection was based on the AIC, and the simpler model was selected even if the removal of a term caused a small increase in AIC ($AIC < 2$). Model fit was examined by inspecting the residuals and checking for any trends. The GLMs fitted for each parasite ranged from simple models including only main interactions, to complex models involving three-way interaction terms. The fitted GLMs were then analysed with an analysis of deviance with chi-square tests, to test for the main effects. Testing was done both on the total dataset ($n=240$) to test for the inter-lake differences, and on the two population datasets ($n=120$) individually, to test for seasonal variation separately within each population.

Statistical analysis was conducted using the software R version 2.12.0 (<http://www.r-project.org/>).

3. RESULTS

3.1. The stickleback populations

The density of sticklebacks in terms of catch per unit effort (CPUE; i.e. number of fish caught per gillnet placed for 24 hours) varied both between populations and months. Catches were highest in Sagelvvatn, with a CPUE of 16 in August, as opposed to only 6 in Takvatn. In both lakes CPUE peaked in August and had lower levels in June and October (Table 1). Stickleback length ranged from 43 to 70 mm (Table 1) with a mean of 57 mm for all samples. Lengths did not differ between populations (Mann-Whitney U-test, $P=0.306$). Seasonal variation in length was found in the Takvatn population (Kruskal-Wallis test, $P=2.565 \cdot 10^{-7}$), but not in Sagelvvatn (Kruskal-Wallis test, $P=0.299$). The overall sex distribution was 86 % females and 14 % males and did not differ significantly between populations (Chi-squared test, $P=0.368$), or between months within either of the two populations (Pearson Chi-squared tests, P -values > 0.274).

Table 1. Summary of the three-spined stickleback samples according to population and month including sample size, mean fish length including standard deviation (S.D.), and catch per unit effort (CPUE; i.e. number of fish caught per gillnet placed for 24 hours).

Population	Month	Sample size	Mean fish length mm (\pm S.D.)	CPUE
Sagelvvatn	June	30	58.1 (\pm 5.8)	1.0
	August	60	57.7 (\pm 3.8)	16.4
	October	30	57.5 (\pm 4.6)	6.7
Takvatn	June	30	61.7 (\pm 4.3)	2.2
	August	60	54.8 (\pm 5.0)	5.6
	October	30	56.6 (\pm 3.8)	0.2

3.2. The parasite communities

A total of 14 macroparasite species, or taxonomic groups, were recovered from different tissues of the three-spined sticklebacks (parasite list Appendix B; pictures Appendix A). The parasite communities were dominated by cestodes and digeneans, and included eight cestodes, one nematode, one monogenean and four digeneans. There was an equal number of auto- and allogenic parasite taxa and a near equal number of specialists and generalists. *Gyrodactylus arcuatus*, *Schistocephalus solidus*, *Proteocephalus* sp1. and were the only stickleback specialists. Two other

specialists were *Cystidicola farionis* and *Eubothrium* sp., being specialists of arctic charr and brown trout. The majority of the parasite taxa were trophically transmitted, with only *G. arcuatus* and the three digeneans; body cavity metacercaria, eye metacercaria and *Diplostomum* spp., being directly transmitted (Appendix B).

The various parasite taxa showed large variations in their distributions, with intensities ranging from one to 450 and prevalences from two to 100 % (Appendix C). Variance to mean ratios ranged from near one in *S. solidus*, to 177 in *Proteocephalus* sp1. which showed the highest degree of overdispersion (Appendix C).

Both the effect of month ($P=0.010$) and population ($P=0.005$) proved significant in the CCA, i.e. month and population proved to account for the differences in parasite abundance at the infra-community level, while sex and length did not. However, only 13.4% of the inertia was accounted for by these two variables, and thus, a lot of the variation in the data remains unexplained. The fact that there was no significant population-month interaction ($P=0.36$) indicates that the temporal variation was similar in the two lakes.

3.3. Inter-lake variation

Of the 14 parasite taxa recorded, 10 were present in both stickleback populations and component-community richness was 11 for Sagelvvatn and 13 for Takvatn (Table 2). *Proteocephalus* sp2. was found only in Sagelvvatn, and *Eubothrium* sp., *Crepidostomum* sp. and *C. farionis* was found only in Takvatn. However, *Eubothrium* sp. was only found in one single fish and therefore abundances did not differ significantly between populations ($P=0.2376$, Appendix E). The parasite taxa not present in both populations, were all autogenic and specialists of brown trout or arctic charr (Appendix B). The remaining autogenic parasite taxa, the stickleback specialists *G. arcuatus* and *Proteocephalus* sp1. and the generalist *Cyathocephalus truncatus* were present in both lakes (Figure 1). The Simpson index indicated higher diversity in the Sagelvvatn stickleback population, and also higher evenness (Table 2). However, these values were very similar. Percentage similarity between the two component-communities was 82 % (Table 2).

Table 2. Parasite component-community and infra-community parameters for the three-spined stickleback populations of Sagelvvatn and Takvatn. Data pooled across months (n=240). CCR is component- and ICR is infra-community species richness.

Population	Component-community				Infra-community		
	Total number of parasites	CCR	Simpson (D-1)	Evenness (D ⁻¹)	Percentage similarity	Parasites per fish (range)	ICR (range)
Sagelvvatn	10 924	11	2.6	0.24	82	87 (9-598)	4.9 (1-9)
Takvatn	6 999	13	2.1	0.16		61 (9-237)	4.7 (2-9)

The total number of parasites was highest in the Sagelvvatn stickleback samples with 10 891 compared to 6 534 in Takvatn (Table 2). The digenean *Diplostomum* spp. was by far the most abundant in both populations with a total abundance of 6 371 and 4 635 for Sagelvvatn and Takvatn, respectively (Figure 1). The remaining parasite taxa varied in total abundance from one to 1 436, many being rare. Overall, all but two parasite taxa (body cavity metacercaria and eye metacercaria) had significantly higher total abundances in Sagelvvatn (Figure 1; Appendix E). The largest inter-lake differences were found between the two autogenic stickleback specialists *G. arcuatus* and *Proteocephalus* sp1., which both had higher abundances in Sagelvvatn (Figure 1). The total number of *Proteocephalus* sp1. was 1 242 in the sample from Sagelvvatn as opposed to only 7 in Takvatnet, and the abundance of *G. arcuatus* was 1 436 in Sagelvvatn and 67 in Takvatn. Encysted metacercaria were more abundant in Takvatn, eye metacercaria with 168 and 391, and body cavity metacercaria with 101 and 172, in Sagelvvatn and Takvatn, respectively (Figure 1). In addition, abundances of the diphylobothrids (i.e. *D. ditremum*, *D. dendriticum* and *Diphylobothrium* spp.) were slightly higher in Sagelvvatn (Figure 1). The four non-shared species all had low abundances in the sticklebacks and a total abundance ranging from one to 16. The only exception was *C. farionis* which had a total abundance of 45 in the Takvatn stickleback population (Figure 1).

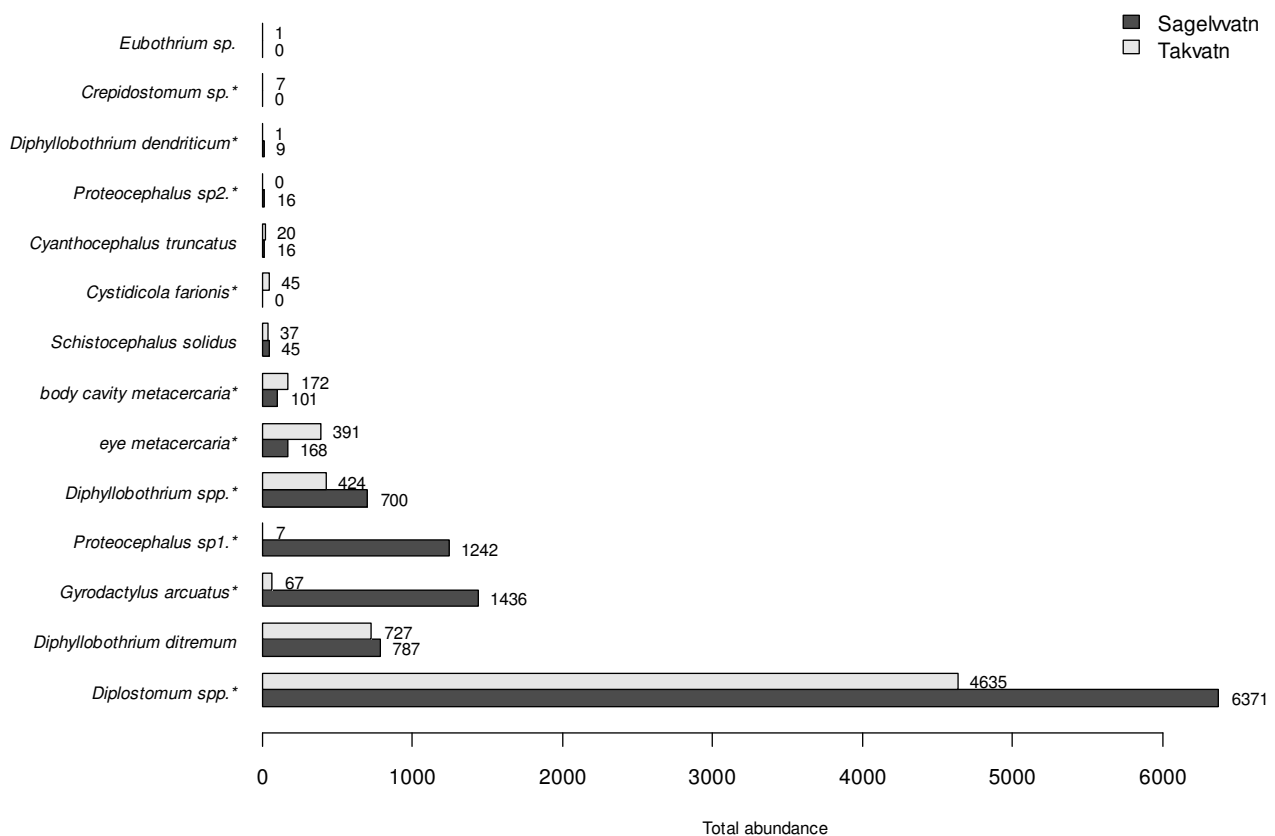


Figure 1. Total abundance of each parasite taxa in the component-communities of sticklebacks from Sagelvvatn and Takvatn. Data pooled across months. Sample sizes are similar (n=120) per lake, allowing for direct comparison. Parasites marked “*” indicate a significant difference in abundances between the individual component-populations, according to Appendix E.

Infra community richness did not differ between the two lakes (Appendix E), with mean levels of ca. 5, ranging from 1 to 9 parasite taxa per fish. Parasite infections were highly aggregated, ranging in intensities from 9 to 598 parasites per fish, and differed between the two populations with a mean number of 87 and 61 for Sagelvvatn and Takvatn, respectively (Table 2; Appendix E).

The nonmetric multidimensional scaling (NMDS) plot of the total parasite abundance data shows, despite some overlap, a segregation of the two stickleback populations (Figure 2). The overlap is due to a great amount of shared species, and the fact that most of the non-shared species are very rare. The non-shared species *Eubothrium* sp., *C. farionis*, *Crepidostomum* sp. and *Proteocephalus* sp2. are all located in the perimeter of the bi-plot along with a few other species since they were found in just a few of the fish, i.e. few fish were characterised as having these parasite taxa in their infra-community. The Sagelvvatn infra-communities were containing higher proportions of *G.*

arcuatus, *Proteocephalus* sp1, diphyllbothrids and *C. truncatus* whereas the Takvatn infra-communities in contrast were containing higher proportions of digeneans (eye and body cavity metacercaria and *Diplostomum* spp.) and *S. solidus*.

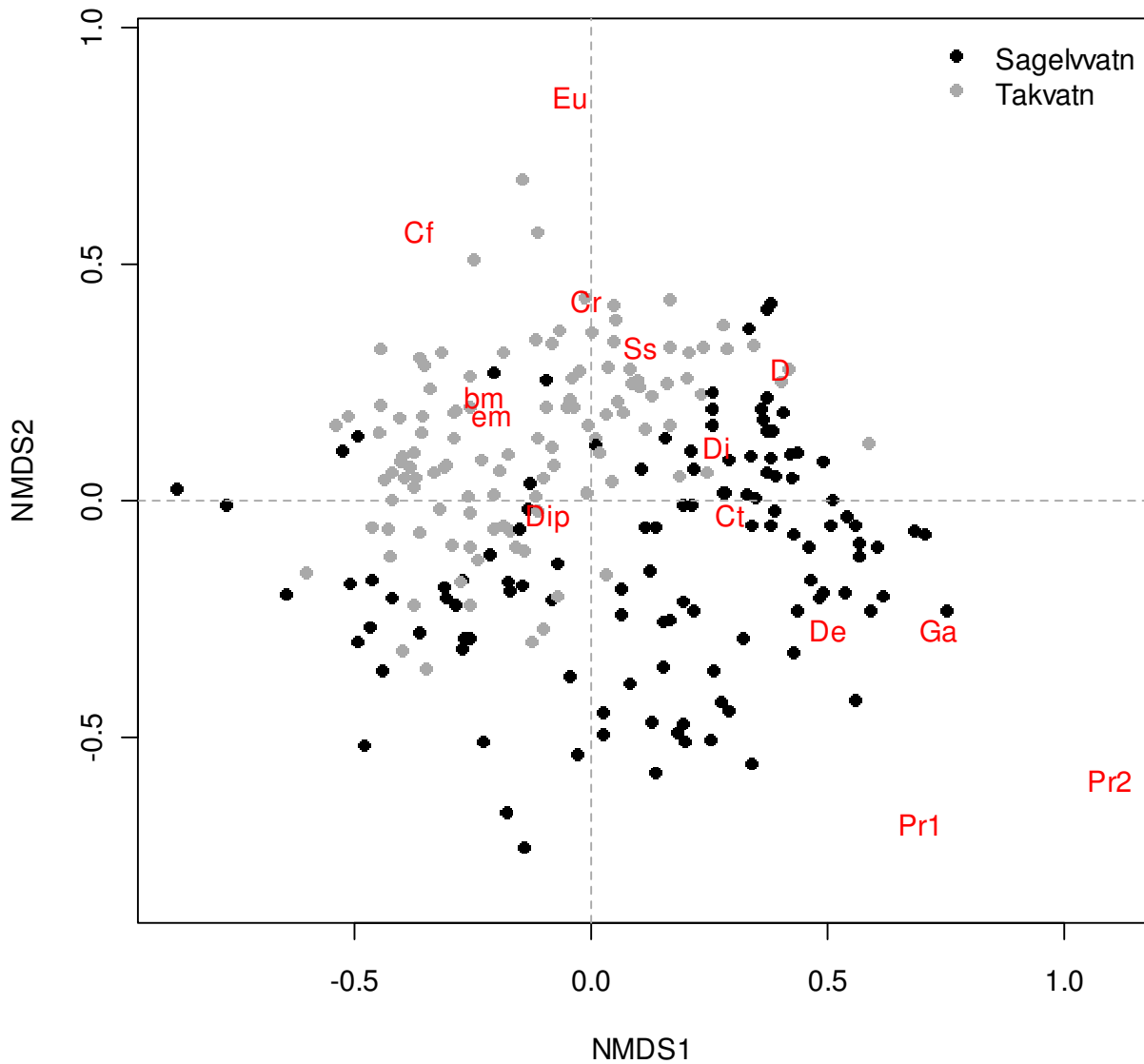


Figure 2. Parasite infra-community composition of the three-spined stickleback populations from Sagelvatn and Takvatn. NMDS bi-plot of Bray-Curtis dissimilarity on log-transformed parasite abundances of the total data (n=240), stress=12.7%. Points represents each fish, and are color coded according to population. Parasite taxa abbreviations: Dip=*Diplostomum* spp., Di=*Diphyllbothrium ditremum*, De= *Diphyllbothrium dendriticum*, D=*Diphyllbothrium* spp., Ga=*Gyrodactylus arcuatus*, Pr1=*Proteocephalus* sp1., em=eye metacercaria, bm=body cavity metacercaria, Ss= *Schistocephalus solidus*, Cf= *Cystidicola farionis*, Ct=*Cyanthocephalus truncatus*, Cr=*Crepidostomum* sp., Pr2=*Proteocephalus* sp2., Eu= *Eubothrium* sp.

On a component-population level, significant inter-lake difference in abundance was found between 10 of the 14 parasite taxa. The only ones that did not differ were *S. solidus*, *Eubothrium* sp., *C. truncatus* and *D. ditremum* (Appendix E). There were no large differences in the prevalence and intensity trends (Figure 3, exact values Appendix C), as low intensity, with a few exceptions, coincided with low prevalence. *G. arcuatus* and *Proteocephalus* sp1., however, had significantly higher prevalence and intensity in Sagelvatn, whereas the eye and body cavity metacercaria stood out as having higher intensity and prevalence in Takvatn.

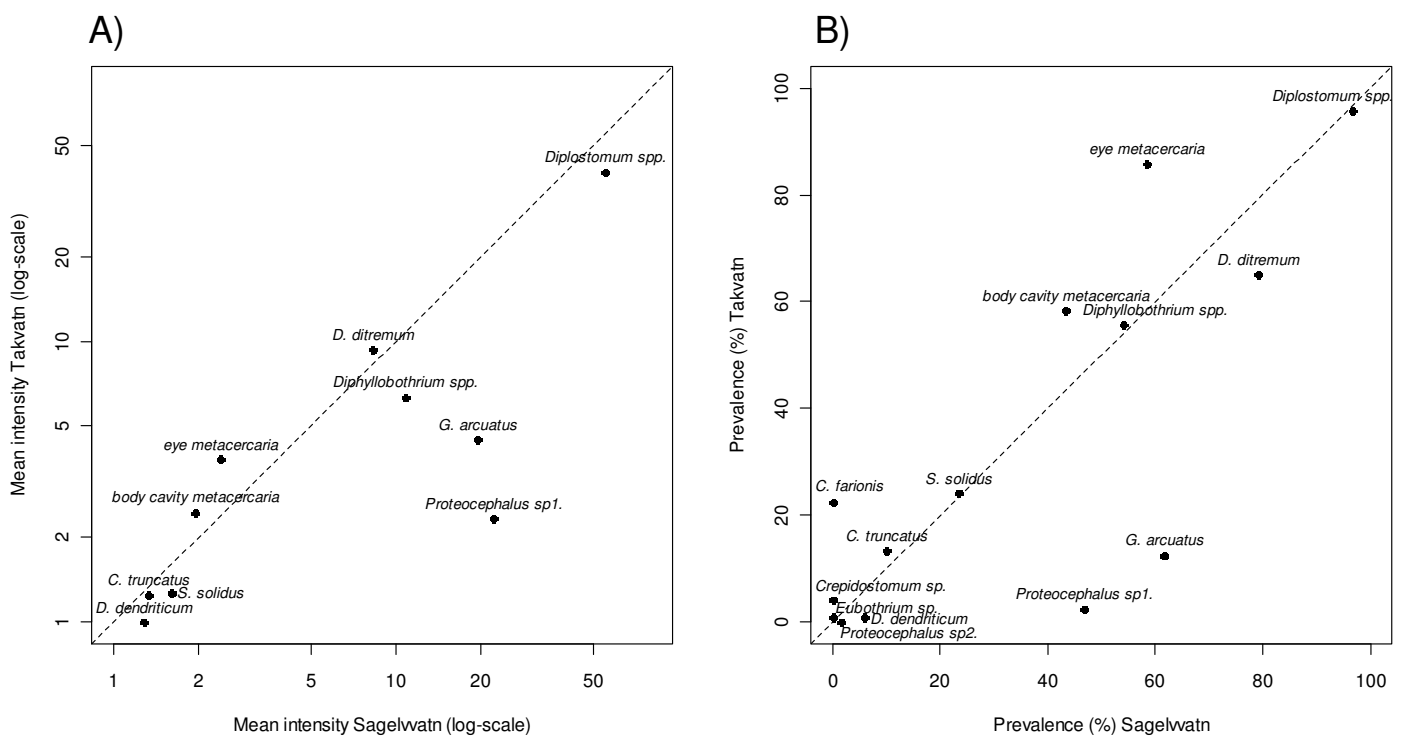


Figure 3. Mean intensity (A) and prevalence (%) (B), of the parasite taxa infecting the three-spined stickleback populations in Sagelvatn (x-axes) and Takvatn (y-axes). Data is pooled across months (n=240). The broken line is the line of equal values between the populations i.e. $x = y$.

3.4. Seasonal variation

Considering the NMDS bi-plots (Figure 4), the seasonal variation revealed a similar pattern in the two lakes although this was more pronounced in Sagelvvatn. In both lakes, the composition of the infra-communities in August was linked to higher relative abundance of the diphyllbothrids (*D. ditremum*, *D. dendriticum* and *Diphyllbothrium* spp.), *G. arcuatus* and *C. truncatus*. In October and June there were higher abundances of digeneans (eye metacercaria, body cavity metacercaria and *Diplostomum* spp.). In June, especially in Sagelvvatn, the parasite infra-populations were intermediate relative to August and October, with no specific parasites dominating the infra-communities. Infra-community richness (ICR) showed to vary significantly between months in both stickleback populations. Number of parasites per fish also varied between the months, but only significantly so in Sagelvvatn (Appendix E). Both ICR and number of parasites per fish showed a seasonal pattern of variation with peak levels in August and lower levels in June and October (Figure 5).

Significant seasonal variation in abundance was found in 11 of the 14 parasite component-populations, however for some of them only in one of the lakes (Appendix E). For *Eubothrium* sp., eye metacercaria and body cavity metacercaria, there was no significant seasonal variation in either of the lakes. The general pattern of seasonal variation consisted of peak abundance in August and lower abundance in June and October. This pattern was most clear for the Sagelvvatn component-populations, while for Takvatn, this pattern was only observed among some of the parasite taxa (Figure 5). Exceptions to this pattern were *C. truncatus* in Sagelvvatn and *C. farionis* in Takvatn, which both declined in mean abundance through the season (Figure 5). Also, *D. ditremum* in Takvatn stood out, by increasing in abundance through the season. Also many of the rare parasites showed no significant seasonal variation (Figure 5; Appendix E).

Prevalences and mean intensities (Appendix F) mostly coincided, and also showed peak levels in August. In some cases, prevalence and intensity did not coincide, as intensities increased while the prevalence decreased (*Proteocephalus* sp1., Sagelvvatn) or vice versa (body cavity metacercaria, Sagelvvatn). The microparasites, sessile ciliate and *Trichodina* sp., had overall high and similar prevalences and intensities (personal observation) through the seasons in both lakes. Only the sessile ciliate showed lower prevalence in June (Appendix F).

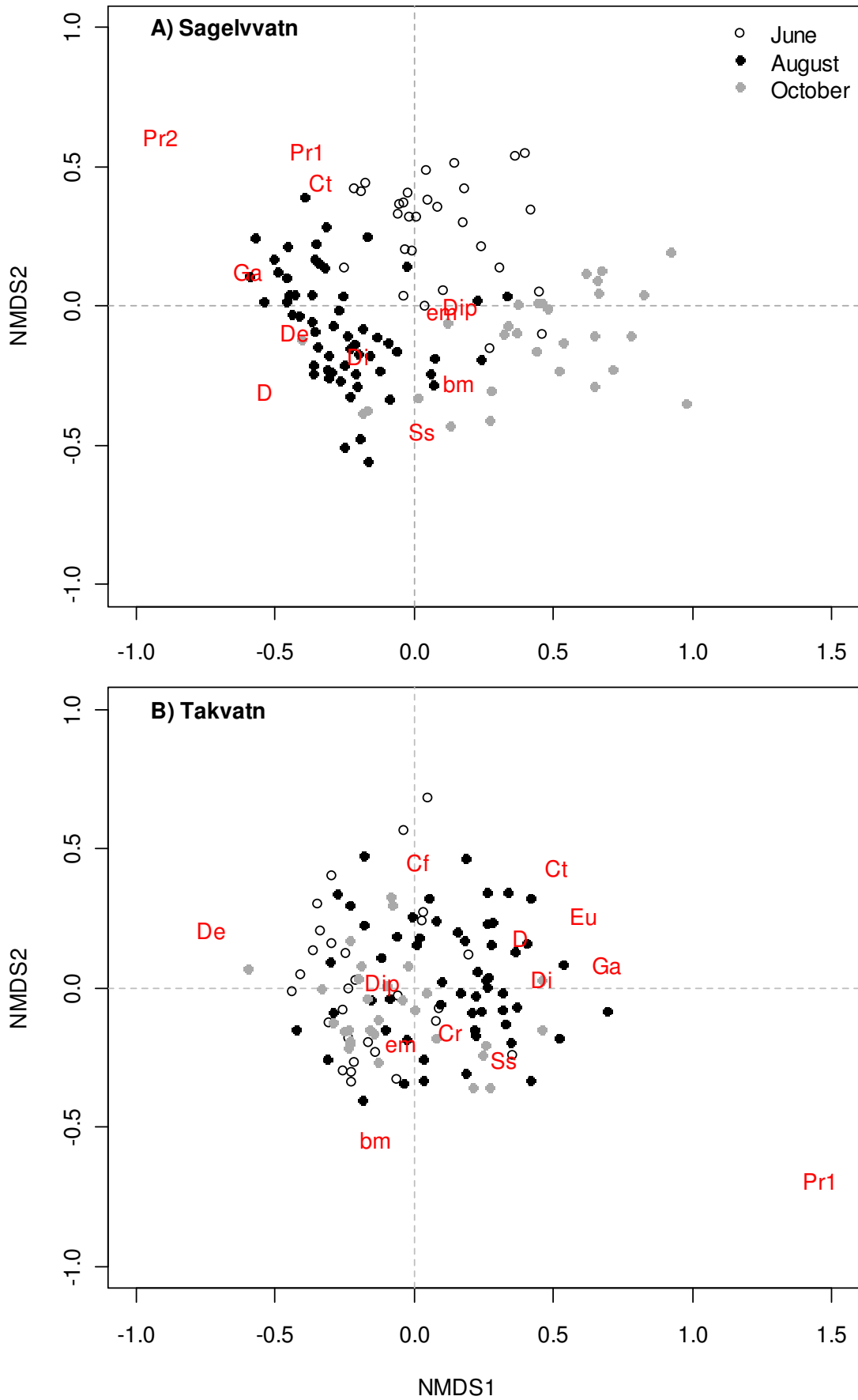


Figure 4. Parasite infra-community composition of the three-spined stickleback populations from (A) Sagelvvatn (n=120) and (B) Takvatn (n=120), showing the seasonal variation. NMDS bi-plot of Bray-Curtis dissimilarity on log-transformed parasite abundances, stress=19%. Points represent each fish, and are color coded according to month. For parasite abbreviations, see Figure 2.

3.5. Sex and length effects

Inter-sex differences in parasite abundance were found only in the newly established diphyllbothrids *Diphyllbothrium* spp. but in both stickleback populations (Appendix E). Seven of the parasite taxa exhibited significant variation in abundance with fish length, although not in all cases in both stickleback populations (Appendix E). The abundances of *C. truncatus*, *D. ditremum*, *Diphyllbothrium* spp., *Crepidostomum* sp., *Diplostomum* spp. and body cavity metacercaria correlated positively with fish length whereas *S. solidus* showed a negative correlation (Derived from effect size of length in the GLMs). Also the number of parasites per fish varied with length in both populations (Appendix E), with a positive correlation (derived from GLM). There was no effect of length on ICR in either population (Appendix E).

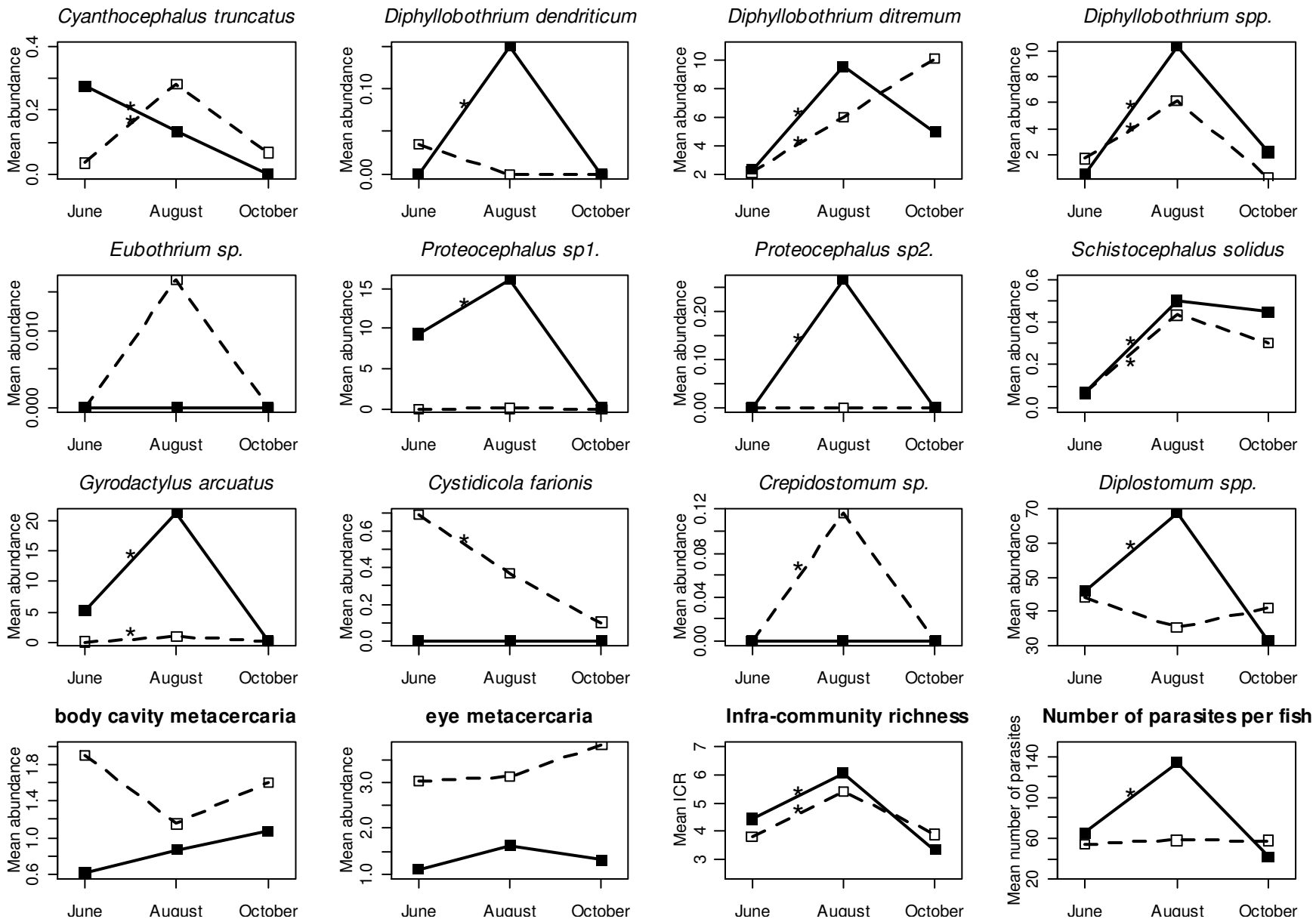


Figure 5. Mean abundance of the different parasite component-populations, mean infra community richness and mean number of parasites per fish for the Sagelvayn (dark dots with unbroken line) and Takvayn (clear dots with broken line) stickleback populations, including the seasonal variation. Significant seasonal variation, are added next to lines according to Appendix E, where “*” equals a P-value < 0.05.

4. DISCUSSION

The present study revealed a very high similarity between the parasite component-communities of the introduced and founder stickleback populations, with only subtle differences in community structure. As expected, all of the allogenic parasite taxa recorded were present in both communities, while all of the autogenic were not. Contrary to the expectation, the introduced Takvatn population had a more species rich parasite community than that of the founder Sagelvvatn population. These subtle differences in species richness, however, can be explained by rare infections in the sticklebacks of parasite taxa infecting sympatric salmonids. Also, two stickleback specialists had been introduced with the sticklebacks into Takvatn thereby further increasing the similarity of the two parasite communities. Parasite abundances were somewhat higher in Sagelvvatn and likely a reflection of higher densities of both main and intermediate hosts. Both species richness and in particular abundances were very high in the two parasite communities compared to similar studies on three-spined sticklebacks (Chappell 1969; Pennycuick 1971b; Kalbe *et al.* 2002). The abundances varied with season among most of the parasite taxa, and with a few exceptions this seasonal variation was similar in the two stickleback populations. Abundances generally peaked in August and were lower in June and October.

As expected, the similarity of the two parasite communities was high, and reflected in both the presence and abundance of the different parasite taxa. The Simpson indexes and Simpson evenness values were slightly higher for the Sagelvvatn component-community indicating the lower presence of rare species. The high percentage similarity underlines the great similarity of the parasite communities, as it indicates that the most common parasite taxa had similar relative abundance in the two communities. Since the two study lakes are situated in geographical proximity to each other, the regional pool of parasites available for colonisation of the two stickleback populations is identical. Furthermore biotic and abiotic factors are assumed to be very similar in the two lakes, adding to increased similarity through supporting equal possibilities for colonisation of a given parasite species. However, as no two lakes are totally alike, small inter-lake variations in biotic factors probably exist with respect to e.g. intermediate host presence and densities, and foraging behaviour of both fish and avian hosts, and these can help explain the observed differences between the two parasite communities.

As expected, all the allogenic parasite taxa recorded were present in both stickleback populations, and accordingly the difference in species richness was explained by autogenic parasite taxa. This is a reflection of the greater dispersal abilities of allogenic parasite species (Kennedy 1976; Esch *et al.* 1988; Fellis and Esch 2005), and it is evident that parasite eggs can be easily dispersed between Sagelvatn and Takvatn by piscivorous birds utilizing both lakes as habitats. Furthermore, all the allogenic parasite taxa found have low host specificity in the adult stage, infecting a large range of piscivorous birds (Chappell 1995; Hoffman 1999). *S. solidus* and *Diplostomum gasterostei* (a stickleback specialist likely included in *Diplostomum* spp.) is the only species that may have been easily dispersed to Takvatn, but only could managed to colonize it following the introduction of their obligatory stickleback host. The other autogenic parasite taxa were generalists infecting other fish species and they were most likely well established in Takvatn before the stickleback introduction. Lastly the generalist *C. truncatus* could possibly have been introduced with the stickleback but is, as it is commonly infecting brown trout and arctic charr, assumed to have been present in Takvatn before the introduction. Furthermore, its low prevalence in the sticklebacks in the present study indicates that it is very unlikely to have been introduced as a hitchhiker.

4.1. Inter-lake differences in parasite species richness

Contrary to other studies on introductions (Torchin *et al.* 2002; Torchin *et al.* 2003; MacLeod *et al.* 2010; Roche *et al.* 2010), the introduced stickleback population in Takvatn was found to harbour a more species rich parasite component-community than the founder Sagelvatn population. The discrepancy is best explained by the successful introduction of the two hitchhiking parasites and to differences in the parasite faunas of sympatric fish species. The present finding is however in line with Ondrackova *et al.* (2010) and Francova *et al.* (2011) who studied parasite communities of round goby (*Neogobius melanostomus*) in native and non-native ranges. They also found the introduced populations to have a slightly more species rich parasite community and the non-common parasite species to have low abundances. They concluded that the local-scale (the Danube River) had led to high similarity of the parasite communities, and that differences were best explained by ecological differences in the habitats. In the present study ecological differences are however small, and many factors that may potentially affect species richness are deemed insignificant.

The two parasite species *Proteocephalus* sp1. and *G. arcuatus* were both autogenic and stickleback specialists which means that they must have colonised Takvatn as hitchhikers with the introduction of their stickleback host. Further, these two species were the only autogenic stickleback specialists present in the founder stickleback population and are therefore restricted to dispersal with their stickleback host. The high prevalence and abundance of these two species in the founder population in Sagelvvatn have likely increased the probability of a successful introduction, assuming that they were similarly high at the time of the introduction. The microparasites *Trichodina* sp. and the sessile ciliate were also found in both populations, but whether these were introduced with the stickleback or not is difficult to assess as these protozoan parasites have low and variable host specificity in addition to a difficult taxonomy (Lom and Dyková 1992). It is therefore possible that they already were present in Takvatn parasitizing arctic charr and brown trout before the introduction of the stickleback. That parasites were not lost during the stickleback host introduction is attributed to the high similarity in environmental factors and the geographical proximity. In addition, the presence of only two autogenic stickleback specialists in the local parasite fauna, have increased similarity in species richness. If there had been a higher numbers autogenic stickleback specialists present in the founder population, then more parasite species could potentially be lost during the introduction of the stickleback host.

Common to the parasite taxa that were not recorded in both stickleback populations (*Proteocephalus* sp2., *Crepidostomum* sp., *Cystidicola farionis* and *Eubothrium* sp.) was in addition to being autogenic that they were specialists of brown trout and, or arctic charr. Further, all had low infections in the sticklebacks, indicating that they were only accidental infections. Parasite species richness can to a large extent be explained by the occurrence of sympatric fish species (Marcogliese and Cone 1991; Fernandez *et al.* 2010), and this seems to be the case in the present study. As the lakes both have the exact same fish communities, the results strongly suggest that these sympatric host species support different parasite communities. It is thus the inter-lake difference in parasite fauna of the sympatric fish species that is reflected in the parasite communities of the sticklebacks. It cannot be ruled out, however, that some of these parasites, while not detected in the sticklebacks, are not present in the parasite communities of the sympatric fish species. It is possible that they are not found among the stickleback samples simply due to low abundances in the sympatric fish populations. With regard to *C. farionis*, however, it is likely not present in Sagelvvatn as it has not

been recorded from its arctic charr host in the lake (P-A. Amundsen, personal communication, November 2011). In addition, when it is present it often occurs at high densities (Knudsen and Klemetsen 1994) and should therefore be expected to be present in the sticklebacks. Since most of these non-common parasites are non-stickleback specialists and occur at low prevalences in the sticklebacks, it is highly unlikely that they could have been introduced as hitchhikers with the stickleback introduction.

In general, ecological factors otherwise leading to differences in species richness were found to have no effect on species richness in the present study, including fish densities (Arneberg *et al.* 1998; Takemoto *et al.* 2005), lake productivity (Esch 1971; Poulin *et al.* 2003), foraging behaviour (Knudsen *et al.* 2004; Valtonen *et al.* 2010) and intermediate host availability (Marcogliese and Cone 1991). While Sagelvatn had both higher fish densities and slightly higher productivity, this was not reflected in higher species richness. Since the differences in host densities and especially productivity were only small, they are regarded as being insufficient in determining parasite species richness. Further, the importance of these mechanisms, are likely reduced due to great ecosystem similarity. The majority of the parasite taxa were trophically transmitted either by amphipods, *Gammarus lacustris* (*C. truncatus*, *C. farionis*, and *Crepidostomum* sp.) or copepods (the remaining cestode species), and marked differences in foraging behaviour between the two stickleback populations on these prey items could affect the species richness (Knudsen and Klemetsen 1994; Valtonen *et al.* 2010). However, the role of foraging behaviour in determining species richness also work in conjunction with differences in presence of, and infection levels in the intermediate hosts. Differences in feeding behaviour are assumed to be minor as the same intermediate host species are assumed to be present in both lakes.

In conclusion it seems that mechanisms that may otherwise contribute to dissimilarity in species richness between parasite communities are of minor importance on a local scale due to high ecosystem similarity. The primary cause of differences in species richness between the two stickleback populations appears to be differences in the parasite communities of the sympatric fish species. Furthermore, the successful introduction of the autogenic stickleback specialists increased similarity, and in addition the fact that there were few autogenic stickleback specialists present in the local parasite fauna that could be lost during the introduction.

4.2. Inter-lake differences in parasite abundance

The overall higher abundances of most of the parasite taxa in Sagelvvatn points however, to some differences between the two lakes. The higher parasite abundances in Sagelvvatn are likely caused by higher densities in the fish populations. Both the density of sticklebacks and sympatric fish species (A. Moe, personal communication, October 2011) were higher in Sagelvvatn, and this could be of great importance in determining inter-lake differences in abundance, as higher densities of both sticklebacks and sympatric fish species would increase parasite transmission rates (Anderson and May 1978; Dobson 1990; Arneberg *et al.* 1998). As many of the most abundant parasite taxa are generalists, the abundances of these may especially be affected by the density of the sympatric fish populations. Other studies have also shown parasite abundances to be positively correlated with productivity (Wiśniewski 1958; Esch 1971), but the differences between the lakes are minor, and the slightly higher productivity in Sagelvvatn is however thought to be related to higher densities of main and intermediate hosts in the lake. In addition, copepod densities were more than twice as high in Sagelvvatn than in Takvatn in August (Skoglund 2011), and as copepods are the intermediate host of all the cestode parasites (Appendix B) this can help explain the higher densities of these in Sagelvvatn. Avian hosts are characterised as harbouring many parasites (Kennedy *et al.* 1986; Poulin and Morand 2000), and as the stickleback is a central prey item in the lakes (Amundsen *et al.* 2009) bird densities are of large importance in determining parasite abundances (Marcogliese *et al.* 2001). The higher parasite densities in Sagelvvatn are thereby thought also to be related to higher densities of piscivorous birds.

The largest inter-lake differences in abundance were found between the two hitchhikers, the autogenic stickleback specialists *Proteocephalus* sp1. and *G. arcuatus*, and can be related to the effects of stickleback and intermediate host densities. The higher copepod abundances can help explain the higher abundance of *Proteocephalus* sp1., as this parasite species utilise copepods as intermediate host. As *G. arcuatus* is directly transmitted, its higher abundances in Sagelvvatn is directly related to the higher host densities (Scott and Anderson 1984; Bakke *et al.* 1996) and to a lesser extent affected by other factors. That the largest inter-lake differences were found among these two species can also be explained partly in their mode of dispersal and host specificity. By being stickleback specialists, their abundances are affected by population dynamics or behaviour of other host species to a lesser extent. Being autogenic means that they are not dispersed by birds

utilizing both habitats. Thereby are inter-lakes similarities in abundances not maintained by a likely high dispersal rate between the lakes in these two parasite species.

An exception to the general pattern of higher parasite abundances in Sagelvvatn was recorded for the encysted metacercaria in the eye and body cavity, which both had highest abundance in Takvatn. As both the *Diplostomum* spp. and the encysted metacercaria utilize lymnaeid snails as their intermediate hosts (Blair 1976; Chappell 1995; Hoffman 1999), the inter-lake differences cannot be explained by differences in intermediate host densities. Neither can it be explained by differences in densities of piscivorous birds. Differences could however be related to differences in habitat use of intermediate and main hosts and is likely a reflection of local variations within each lake.

Lastly, differences in stickleback foraging behaviour may partly explain differences in the abundances of trophically transmitted parasites (Knudsen *et al.* 2004; Valtonen *et al.* 2010). If one ignores the non-shared parasite taxa, there was no difference in abundance in the amphipod transmitted parasites. However, the abundance of all the copepod transmitted parasites was higher in the Sagelvvatn parasite community, which corresponds well to the higher density of this intermediate host in the lake. Whether the observed differences in abundance were caused by differences in intermediate host densities, or in foraging behaviour, is difficult to infer as both factors influence the acquisition of parasites. Food preference vary with food availability as prey items (and intermediate hosts) of higher densities are selectively preyed upon by the three-spined stickleback (Visser 1982), thereby linking foraging behaviour closely to intermediate host densities.

4.3. Seasonal variation in parasite abundance

The abundances of the parasite component-populations changed with the sampling periods, and hence did also the composition of the infra-communities. With a few exceptions, the seasonal changes in parasite abundances were similar in the two stickleback populations, however more pronounced in Sagelvvatn. An explanation to the general trend is an accumulation due to new infections throughout the season and a decrease due to host mortality in late summer.

Parasites accumulate over time (Morand 2000) and endoparasites persist in the stickleback host following infection with exception of those residing in the intestine (Appendix B) as they dislodge following reproduction. The total number of parasites per fish correlated positively with fish length, as has been documented in other studies (e.g. Fellis and Esch 2004), and the higher number of parasites in longer fish is a result of accumulation over time as length correlates with age. Accumulation is further enhanced by increasing food consumption rates in larger and older fish, and thus increased exposure to trophically transmitted parasites (Morand and Poulin 1998; Fellis and Esch 2004; Poulin and Leung 2011). The accumulation of parasites in the sticklebacks in the present study was reflected in that some of the parasite component-populations and the total number of parasites per fish correlated positively with fish length.

The amount of new infections vary depending on exposure to infective stages (Esch and Fernández 1993; Sandland *et al.* 2001), and this exposure vary with differences in biotic and abiotic factors. Abiotic factors includes temperature, and as release of digenean cercaria from snail intermediate hosts increases at higher temperatures (Fried *et al.* 2002), this would lead to a peak in new infections in mid summer. Of further importance are biotic factors such as intermediate and final host densities. In Takvatn, copepod densities decline through the summer (Primicerio and Klemetsen 1999) and this could affect the amount of newly established cestodes utilising copepods as intermediate hosts, and be reflected in the newly established diphyllbothrids *Diphyllbothrium* spp. Also the densities of main fish and avian hosts affects transmission rates through a higher release of parasite eggs. Foraging behaviour will also effect the exposure to infective stages, and in general an increase in abundances in summer is likely enhanced by higher food consumption at higher temperatures (Östlund-Nilsson *et al.* 2007). Higher food consumption in summer might be of particular importance in the present study, as northern ecosystems have shorter growth season, which could enhance the seasonal effects.

In the short lived three-spined stickleback mortality rates are high (Wootton 1984) and often induced by parasites, especially by the cestode *S. solidus* (Pennycuick 1971a; Tierney *et al.* 1996; Bagamian *et al.* 2004; Barber and Scharsack 2010). Reduction in fitness in the fish host has also been documented among diplostomids (Brassard *et al.* 1982; Owen *et al.* 1993), diphyllbothrids (Bylund 1972; Rahkonen *et al.* 1996) and encysted metacercaria (*Apatemon gracilis*, Gordon and Rau 1982). Upon dissection of the sticklebacks, some of the most heavily infected specimens were

observed to have very low liver volume and hence energy reserves in line with observations by Arme and Owen (1967), supporting that heavy parasite infections have a negative effect on stickleback fitness in the present study. It is therefore reason to believe that a positive correlation between host mortality rates and parasite intensities exists, and that this in large part explains the observed lower parasite abundances in the autumn. This increased mortality among the most heavily infected fish is further supported by a decrease in the variance-mean ratio in October recorded for many of the most overdispersed parasite taxa (Gordon and Rau 1982; Knudsen *et al.* 2002). Sticklebacks stagnate in growth after reaching maturity, and based on the length data from previous studies of the Takvatn stickleback population (Pedersen 1987) all fish samples included specimens of both 2, 3 and 4 year old fish. The proportion of older fish (3 and 4 years) in the samples can be assumed to decrease throughout the summer due to the higher mortality rates among older fish. The decrease in abundances in late summer can thereby be explained by a decrease in the proportion of the oldest individuals with high intensities of accumulated parasites.

In Takvatn, more parasite component-populations departed from the general pattern of higher abundances in August or showed no significant seasonal variation. This was also reflected in smaller variations in the infra-community composition. An explanation to these differences may be found among differences in both the frequency of new infections and stickleback mortality rates. It is likely that higher host densities and higher parasite abundances have led to higher mortality rates in the Sagelvvatn stickleback population. In general, an increase in accumulated parasites with season was only observed early in summer, and the decrease in late summer is best explained by an increase in host mortality rates. The seasonal variation in the infra-community composition revealed by the nonmetric multidimensional scaling (NMDS) bi-plots can also be seen in relation to the high late summer host mortality. Apart from *S. solidus*, the trematodes dominated the October infra-communities, and as these are all smaller and less pathogenic they dominate in the surviving sticklebacks. The parasites dominating in August in both lakes are the larger diphyllbothrids which probably have a stronger negative effect on host survival than the other parasite taxa. With regard to the highly pathogenic *S. solidus*, however, the parasite induced mortality in sticklebacks is highest in autumn (Pennycuick 1971b), and the time of the October sampling assumed to have coincided with high infection levels. Due to the high pathogenicity many of the *S. solidus* infected fish will most likely die out during the autumn.

The seasonal variation in the stickleback parasite abundances in the present study was a reflection of both the acquisition and accumulation of new parasites during the season and high host mortality rates in late summer. The affect of accumulation of parasites and host mortality, and sampling on different age classes however, can be difficult to tell apart. The results suggests that parasite accumulate through the season, but that high mortality rates and the sampling on younger age classes with fewer accumulated parasites are of major influence in explaining the late summer decrease in parasite abundances.

5. CONCLUSION

The study revealed high similarity in the parasite communities of the introduced and founder stickleback populations. The high similarity was explained by the geographical proximity and high similarity of the ecosystems, and hence biotic and abiotic factors. Similarity was further enhanced by the successful introduction of two hitchhiking parasites. The stickleback introduction had in addition allowed for the further colonisation of the introduced population by two other parasite species from the founder stickleback population, through dispersal by avian hosts. The high similarity of the parasites communities was further enhanced by the presence of few stickleback generalists in the founder population that could potentially be lost during the host introduction. The subtle difference in species richness between the two parasite communities could be explained by accidental infections by parasite species of sympatric fish hosts, underlining the importance of sympatric host species and their parasite faunas in determining parasite species richness.

One observed difference between the ecosystems was in fish host densities, which is suggested as the primary cause of the difference in parasite abundance between the two stickleback populations. The seasonal variation was partly an effect of the accumulation of parasites, but it seem strongly affected by an increase in host mortality among the most parasitized sticklebacks in late summer, and due to sampling on different age classes.

In general, the great ecosystem similarity and the local scale allowed for a study less confounded by a large range of factors otherwise increasing dissimilarity in parasite communities. This resulted thereby in a more specific study on the effects of dispersal mechanisms and host introductions. The main conclusion is that many of the mechanisms otherwise influencing parasite communities are of lesser importance on a local scale. Accordingly it shows that local scale fish introductions are more likely to bring along hitchhiking parasites.

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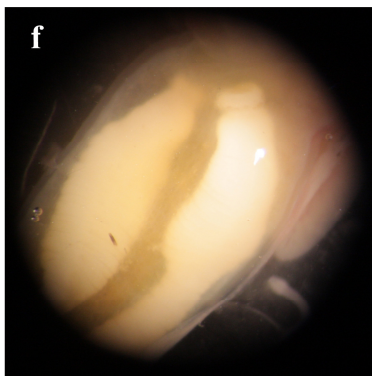
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8. APPENDIXES

Appendix A. A selection of the different parasites (groups or species) collected from the Sagelvatn and Takvatn three-spined sticklebacks: a) larger *Diplostomum* sp., b) encysted metacercaria from eye (similar to those found in the body cavity), c) smaller *Diplostomum* sp., d) *Proteocephalus* sp1., e) *Schistocephalus solidus*, f) *Cyathocephalus truncatus* attached to intestine, g) *Cystidicola farionis*, h) *Proteocephalus* sp2.



Appendix B. Parasites infecting the three-spined sticklebacks in Sagelvvatn and Takvatn grouped by taxon. Location in host, stage of development, lifecycle type, transmission route, host specificity and hosts is indicated. "*" indicates autogenic (i.e. within lake) lifecycle and "--" indicates allogenic lifecycle (i.e. mature in birds). G and S refers to generalist and specialist.

References: Sterud (1999) and Levsen (1992).

	Group	Species or taxon	Location	Stage	Lifecycle	Transmission	Specialist/generalist	Host(s)
Macroparasites	Cestoda	<i>Cyathocephalus truncatus</i>	intestine	adult	*	amphipod	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		<i>Diphyllobothrium dendriticum</i>	liver, body cavity, encysted in stomach wall	plerocercoid	-	copepod	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		<i>Diphyllobothrium ditremum</i>	liver, body cavity, encysted in stomach wall	plerocercoid	-	copepod	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		<i>Diphyllobothrium</i> spp.	liver, body cavity, encysted in stomach wall	plerocercoid	-	copepod	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		<i>Eubothrium</i> sp.	intestine	adult	*	copepod	S	<i>S. alpinus</i> or <i>S. trutta</i>
		<i>Proteocephalus</i> sp1.	intestine	plerocercoid	*	copepod	S	<i>G. aculeatus</i> (<i>P. Filicollis</i>)
		<i>Proteocephalus</i> sp2.	intestine	plerocercoid	*	copepod	S	<i>S. alpinus</i> or <i>S. trutta</i>
		<i>Schistocephalus solidus</i>	body cavity	plerocercoid	-	copepod	S	<i>G. aculeatus</i>
	Monogenea	<i>Gyrodactylus arcuatus</i>	skin, fins	adult	*	direct	S	<i>G. aculeatus</i>
	Nematoda	<i>Cystidicola farionis</i>	swimbladder	small adult	*	amphipod	S	<i>S. alpinus</i>
	Digenea	<i>Crepidostomum</i> sp.	intestine	adult	*	amphipod	G	<i>S. alpinus</i> , <i>S. trutta</i>
		<i>Diplostomum</i> spp.	eye	metacercaria	-	direct	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		body cavity metacercaria	body cavity	metacercaria	-	direct	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
		eye metacercaria	eye	metacercaria	-	direct	G	<i>S. alpinus</i> , <i>S. trutta</i> , <i>G. aculeatus</i>
Microparasites	Protozoa	<i>Trichodina</i> sp.	skin, fins	-	*	direct	G	?
		sessile ciliate	skin, fins	-	*	direct	G	?

Appendix C. Inter-lake parameters. Total abundance, prevalence (%), mean intensity (range), mean abundance (\pm S.D.) and variance to mean ratio of the parasite component-populations of the three-spined sticklebacks in Sagelvvatn and Takvatn.

Species /group	Population	Total abundance	Prevalence (%)	Mean intensity (range)	Mean abundance (\pmS.D.)	Variance/mean ratio
<i>Cyathocephalus truncatus</i>	Sagelvvatn	16	10.3	1.3 (1-2)	0.140 (\pm 0.435)	1.4
	Takvatn	20	13.9	1.3 (1-2)	0.174 (\pm 0.464)	1.2
<i>Diphyllobothrium dendriticum</i>	Sagelvvatn	9	6.0	1.3 (1-2)	0.076 (\pm 0.327)	1.4
	Takvatn	1	0.9	1.0 (1)	0.009 (\pm 0.093)	1.0
<i>Diphyllobothrium ditremum</i>	Sagelvvatn	787	81.9	8.3 (1-60)	6.784 (\pm 10.233)	15.4
	Takvatn	727	67.8	9.3 (1-128)	6.322 (\pm 14.299)	32.3
<i>Diphyllobothrium</i> spp.	Sagelvvatn	700	56.0	10.8 (1-34)	6.034 (\pm 8.235)	11.2
	Takvatn	424	58.3	6.3 (1-78)	3.687 (\pm 9.215)	23.0
<i>Eubothrium</i> sp.	Sagelvvatn	0	0	-	0	-
	Takvatn	1	0.9	1.0 (1)	0.009 (\pm 0.093)	1.0
<i>Proteocephalus</i> sp1.	Sagelvvatn	1242	48.3	22.2 (1-450)	10.710 (\pm 43.544)	177.1
	Takvatn	7	2.6	2.3 (1-4)	0.061 (\pm 0.825)	3.0
<i>Proteocephalus</i> sp2.	Sagelvvatn	16	1.7	8.0 (1-15)	0.138 (\pm 1.395)	14.1
	Takvatn	0	0	-	0	-
<i>Schistocephalus solidus</i>	Sagelvvatn	45	24.1	1.6 (1-4)	0.388 (\pm 0.810)	1.7
	Takvatn	37	25.2	1.3 (1-3)	0.322 (\pm 0.629)	1.2
<i>Gyrodactylus arcuatus</i>	Sagelvvatn	1436	63.8	19.4 (1-225)	12.379 (\pm 30.648)	75.9
	Takvatn	67	13.0	4.5 (1-27)	0.583 (\pm 2.785)	13.3
<i>Cystidicola farionis</i>	Sagelvvatn	0	0	-	0	-
	Takvatn	45	23.5	1.7 (1-5)	0.391 (\pm 0.886)	2.0
<i>Crepidostomum</i> sp.	Sagelvvatn	0	0	-	0	-
	Takvatn	7	4.4	1.4 (1-2)	0.061 (\pm 0.305)	1.5
<i>Diplostomum</i> spp.	Sagelvvatn	6371	100.0	55.0 (7-151)	54.922 (\pm 28.000)	14.3
	Takvatn	4635	100.0	40.3 (11-151)	40.304 (\pm 22.250)	12.3
body cavity metacercaria	Sagelvvatn	101	44.8	1.9 (1-13)	0.871 (\pm 1.580)	2.9
	Takvatn	172	60.9	2.5 (1-9)	1.496 (\pm 1.970)	2.6
eye metacercaria	Sagelvvatn	168	60.3	2.4 (1-13)	1.448 (\pm 1.917)	2.5
	Takvatn	391	89.6	3.8 (1-10)	3.400 (\pm 2.467)	1.8
<i>Trichodina</i> sp.	Sagelvvatn	-	96.0	-	-	-
	Takvatn	-	88.7	-	-	-
sessile ciliate	Sagelvvatn	-	70.4	-	-	-
	Takvatn	-	69.6	-	-	-

Appendix D. Seasonal variation parameters. Prevalence (%), mean intensity (range) and variance to mean ratio of the parasite component populations of the three-spined sticklebacks in Sagelvvatn and Takvatn.

Species/group	Population	Prevalence (%)			Mean intensity (range)			Variance/mean ratio		
		June	August	October	June	August	October	June	August	October
<i>Cyathocephalus truncatus</i>	Sagelvvatn	20.0	10.0	-	1.3 (1-2)	1.3 (1-2)	-	1.3	1.4	-
	Takvatn	3.3	21.7	6.7	1.0 (1-1)	1.3 (1-2)	1 (1-1)	1.0	1.2	1.0
<i>Diphyllobothrium dendriticum</i>	Sagelvvatn	-	11.7	-	-	1.3 (1-2)	-	-	1.3	-
	Takvatn	3.3	-	-	1.0 (1-1)	-	-	1.0	-	-
<i>Diphyllobothrium ditremum</i>	Sagelvvatn	83.3	90.0	66.7	2.8 (1-6)	11.1 (1-60)	8.3 (1-59)	1.6	11.9	25.7
	Takvatn	33.3	85.0	73.3	6.3 (1-38)	8.0 (1-32)	13.8 (1-128)	24.3	8.4	6.9
<i>Diphyllobothrium</i> spp	Sagelvvatn	10.0	91.7	30.0	4.7 (2-7)	11.6 (1-34)	7.7 (1-33)	5.3	6.5	17.6
	Takvatn	63.3	85.0	6.7	2.9 (1-7)	8.0 (1-78)	2.5 (2-3)	2.6	21.9	2.5
<i>Eubothrium</i> sp.	Sagelvvatn	-	-	-	-	-	-	-	-	-
	Takvatn	-	1.7	-	-	1.0 (1-1)	-	-	1.0	-
<i>Proteocephalus</i> sp1.	Sagelvvatn	80.0	50.0	10.0	11.3 (1-35)	32.1 (1-450)	3.0 (1-6)	10.8	222.1	4.4
	Takvatn	-	5.0	-	-	2.3 (1-4)	-	-	2.9	-
<i>Proteocephalus</i> sp2.	Sagelvvatn	-	3.3	-	-	8.0 (1-15)	-	-	14.1	-
	Takvatn	-	-	-	-	-	-	-	-	-
<i>Schistocephalus solidus</i>	Sagelvvatn	10.0	30.0	33.3	1.0 (1-1)	1.7 (1-4)	1.4 (1-2)	0.9	1.8	1.1
	Takvatn	6.7	41.7	20.0	1.0 (1-1)	1.2 (1-3)	1.5 (1-3)	1.0	1.0	1.6
<i>Gyrodactylus arcuatus</i>	Sagelvvatn	60.0	90.0	13.3	8.8 (1-50)	25 (1-225)	1.8 (1-4)	27.3	72.1	2.6
	Takvatn	3.3	20.0	10.0	1.0 (1-1)	5.1 (1-27)	2.3 (2-3)	1.0	14.1	2.3
<i>Cystidicola farionis</i>	Sagelvvatn	-	-	-	-	-	-	-	-	-
	Takvatn	40.0	25.0	6.7	1.8 (1-5)	1.5 (1-3)	1.5 (1-2)	2.1	1.7	1.6
<i>Crepidostomum</i> sp.	Sagelvvatn	-	-	-	-	-	-	-	-	-
	Takvatn	-	10.0	-	-	1.2 (1-2)	-	-	1.4	-
<i>Diplostomum</i> spp.	Sagelvvatn	100.0	100.0	100.0	46.1 (13-102)	70.8 (24-151)	33.1 (7-79)	9.2	8.9	11.1
	Takvatn	100.0	100.0	100.0	44.8 (11-100)	37.6 (11-151)	41.1 (18-80)	9.4	16.9	6.8
body cavity metacercaria	Sagelvvatn	20.0	58.3	43.3	3 (1-6)	1.5 (1-3)	2.6 (1-13)	3.3	1.0	5.5
	Takvatn	53.3	58.3	73.3	3.6 (1-9)	2.1 (1-8)	2.2 (1-7)	3.4	2.3	1.9
eye metacercaria	Sagelvvatn	63.3	64.4	50.0	1.7 (1-4)	2.6 (1-7)	2.8 (1-13)	1.2	2.0	4.8
	Takvatn	83.3	91.2	93.3	3.6 (1-9)	3.6 (1-10)	4.1 (1-10)	1.9	1.6	2.0
<i>Trichodina</i> sp.	Sagelvvatn	90.0	96.7	96.7	-	-	-	-	-	-
	Takvatn	93.3	91.7	83.3	-	-	-	-	-	-
sessile ciliate	Sagelvvatn	13.3	88.3	90.0	-	-	-	-	-	-
	Takvatn	26.7	83.3	86.7	-	-	-	-	-	-

Appendix E. Anova test results of the GLMs of the parasite abundances. Res. dev. is the residual deviance and P is the P-value. Significance levels are indicated as: *** = P<0.001, ** = P<0.01, * = P<0.05, . = P<0.10 and - = P>0.10. Blanks indicate that the effect was not included in the model. The population effect is tested on the total data set (n=240), while month, length and sex are tested on the intra-lake data separately (n=120). Test results are showed only for the main terms despite the presence of significant interactions.

		Population		Month		Length		Sex	
		P	Res. dev.	P	Res. dev.	P	Res. dev.	P	Res. dev.
<i>Cyathocephalus truncatus</i>	Sagelvatn	-		*	41.6				
	Takvatn			**	69.2	***	55.4	.	51.6
<i>Diphyllobothrium dendriticum</i>	Sagelvatn	**	50.4	**	31.3	.	28.5		
	Takvatn			-					
<i>Diphyllobothrium ditremum</i>	Sagelvatn	-		***	173.2	***	160.6		
	Takvatn			**	122.1				
<i>Diphyllobothrium</i> spp.	Sagelvatn	***	440.1	***	197.3	***	156.4	***	148.5
	Takvatn			***	197.4	***	156.4	***	148.5
<i>Eubothrium</i> sp.	Sagelvatn	-							
<i>Proteocephalus</i> sp1.	Sagelvatn	***	162.6	***	108.0			.	104.4
	Takvatn					.	9.0		
<i>Proteocephalus</i> sp2.	Sagelvatn	***	144.6	***	122.4	-		-	
	Takvatn								
<i>Schistocephalus solidus</i>	Sagelvatn	-		**	75.5	-			
	Takvatn			**	96.5	***	80.3		
<i>Gyrodactylus arcuatus</i>	Sagelvatn	***	290.6	***	121.4	-			
	Takvatn			**	46.7	-			
<i>Cystidicola farionis</i>	Sagelvatn	***	81.1						
	Takvatn			*	72.2				
<i>Crepidostomum</i> sp.	Sagelvatn	**	31.9						
	Takvatn			*	22.8	*	17.6		
<i>Diplostomum</i> spp.	Sagelvatn	***	373.1	***	145.2	***	130.6		
	Takvatn			-		***	119.3		
body cavity metacercaria	Sagelvatn	**	246.3	-		-			
	Takvatn			-		*	127.6	-	
eye metacercaria	Sagelvatn	***	282.7					-	
	Takvatn					-			
Infra community richness	Sagelvatn	-		***	89.4				
	Takvatn			***	51.6				
Number of parasites per fish	Sagelvatn	***	387.0	***	145.0	***	129.1		
	Takvatn			-		***	117.6		

Appendix F. Prevalence (bars) and mean intensity (dots and lines) for the different parasite component-populations of the Sagelvvann (dark bars, dark dots with unbroken line) and Takvann (light bars, clear dots with broken line) three-spined stickleback populations.

