Parasites of resident arctic charr, Salvelinus alpinus, and brown trout, Salmo trutta, in two lakes in Iceland

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ABSTRACT

Arctic charr and brown trout in two dissimilar lakes in Iceland were examined for parasites, altogether 40 fish, 10 of each species in each lake. At least 22 parasite species were found; Protozoa: Spironucleus salmonis, Apiosoma sp., Capriniana piscium, Trichodina sp., Dermocystidium branchiale; Myxozoa: Chloromyxum truttae, Myxidium truttae, Myxobolus arcticus, M. cerebralis, M. neurobius, Sphaerospora truttae; Helminths: Apatemon gracilis, Diplostomum sp., Crepidostomum farionis, Phyllodistomum conostomum, Diphyllobothrium sp., Eubothrium crassum, E. salvelini, Philonema oncorhynchi, Capillaria salvelini; Crustacea: Salmincola edwardsii and Salmincola (salmonea) sp. Six of the observed species are new records in Icelandic freshwater fish. In general, the total parasite fauna of the two lakes showed a high degree of similarity, both with regards to micro- and macro-parasites. The majority of species were found in both lakes and many in/on both fish species. However, a considerable variability in prevalence and intensity between lakes and/or fish species was evident for certain parasite species. The results of the present study are compared with other similar studies in Iceland as well with the occurrence of the parasite species in neighbouring countries.

Keywords: Arctic charr, brown trout, parasites, Iceland

YFIRLIT

Sníkjudýr staðbundinnar bleikju og urriða í Elliðavatni og Hafravatni

Leitað var að sníkjudýrum í urriða og bleikju í tveim ólíkum íslenskum vötnum, alls 40 fiskum, 10 af hvorri tegund í hvoru vatni. Að minnsta kosti 22 tegundir fundust; Frumdýr: *Spironucleus salmonis, Apiosoma* sp. *Capriniana piscium, Trichodina* sp., *Dermocystidium branchiale*; Slímdýr: *Chloromyxum truttae, Myxidium truttae, Myxobolus arcticus, M. cerebralis, M. neurobius, Sphaerospora truttae*; Flatormar: *Apatemon gracilis, Diplostomum* sp., *Crepidostomum farionis, Phyllodistomum conostomum, Diphyllobothrium* sp., *Eubothrium crassum, E. salvelini*; Práðormar: *Philonema oncorhynchi, Capillaria salvelini*; Krabbadýr: *Salmincola edwardsii og Salmincola (salmonea)* sp. Sex tegundanna höfðu ekki fundist áður á Íslandi. Almennt má segja að sníkjudýrafánan í báðum vötnum hafi verið talsvert lík, bæði hvað varðar smásæ og stærri sníkjudýr. Flestar tegundirnar fundust í báðum vötnum og margar í eða á báðum fisktegundum. Aftur á

móti var greinilega talsverður breytileiki í tíðni og magni milli vatna og/eða fisktegunda hvað varðaði sumar sníkjudýrategundirnar. Niðurstöður rannsóknarinnar eru bornar saman við aðrar svipaðar rannsóknir á Íslandi og við tilvist sníkjudýrategundanna í nágrannalöndunum.

INTRODUCTION

Five species of fishes inhabit the Icelandic freshwater ecosystem: Atlantic salmon Salmo salar L., brown trout Salmo trutta L., arctic charr Salvelinus alpinus (L.), three-spined stickleback Gasterosteus aculeatus L. and eel Anguilla anguilla (L.). Most of the earlier parasitological studies on freshwater fishes in Iceland focused on particular parasite species or certain groups of parasites (Stephensen 1940, Brinckmann 1956, Blair 1973, Blair 1976) and until the 1980's, no systematic research on the total parasite fauna of freshwater fishes had been made. In 1981-1982 four review articles on parasites of Icelandic salmonids were published (Richter 1981, 1982a, 1982b, 1982c). These papers were based on the author's examinations as well as on all data on parasites of Icelandic salmonids available at that time. Since then only a few systematic studies have been performed: a study of the parasite fauna of arctic charr and brown trout from Lake Selvatn (Stefánsson 1986), two studies of metazoan parasites of arctic charr in Lake Thingvallavatn (Malmquist et al. 1986, Frandsen et al. 1989), preliminary observations of the parasite fauna of three-spined sticklebacks (Richter 2003) and a study of eel parasites (Kristmundsson & Helgason 2007). In addition, a number of ecological studies of fish populations of various lakes in Iceland have been performed by the Institute of Freshwater Fisheries and the Institute of Biology, University of Iceland, in which certain macroscopic parasites, detectable with the naked eye, have been reported (e. g. Kristjánsson & Gíslason 1984, Antonsson & Gudbergsson 2000, Jónsson 2000, Björnsson 2002, Jónsson & Gudbergsson 2003, Jónsson et al. 2006). These studies, however, only give a rough estimate of the prevalence of certain parasite species.

The aim of the present study was to survey the most common parasites of resident brown trout and arctic charr in two dissimilar lakes in Iceland. A special emphasis was made to detect microparasites, which to date have been poorly studied. Additionally, an attempt was made to analyse the variation of the parasite fauna between the two lakes and the two fish species.

MATERIALS AND METHODS

Fish were caught, using either fyke- or gillnets, from two lakes in SW Iceland: 1) Ellidavatn (EV): area approximately 2 km², mean depth 1.5 m, maximum depth less than 2-3 m, clay bottom and water volume approximately 3 million m3. Two rivers flow into the lake and there is a 6.0 km long outlet river flowing into the sea. 2) Hafravatn (HV): Area approximately 1 km², mean depth 8 m, maximum depth 28 m, water volume approximately 8 million m³, stony shoreline. A river flows into the lake and there is a 10.4 km long outlet river flowing into the sea. The lakes are approximately 6 km apart and the shortest marine distance between the outlets is approximately 10 km. Other fish species found in these lakes are three-spined stickleback, eel and migrating salmon.

Five fish of each species, arctic charr and brown trout, were caught in both lakes during the autumn (Sept.-Nov.) of 2002 and 2003 and the same number of both fish species in the spring (May-June) of 2005 for a total of 20 brown trout and 20 arctic charr. There was a marked difference in length compared to age between the fish caught for the study, the fish in HV being substantially smaller (Figure 1).

The fish were brought alive to the laboratory and either examined immediately, kept alive in aquaria until they were examined (completed within 3 days to a few weeks of capture) or slaughtered and kept frozen at -20°C for subsequent examination. In the case of freezing (17 fish), gills, external surface, mouth cavity and blood samples were examined prior to freezing.

The length of the fish was measured and otoliths were collected for age determination.

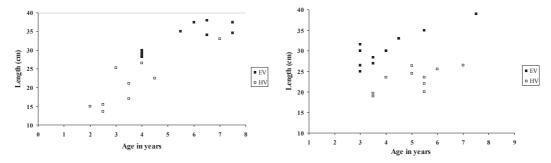


Figure 1. Age-length relationship of brown trout (left) and arctic charr sampled in Elliðavatn (EV) and Hafravatn (HV).

Blood smears were prepared, fixed in methanol, stained with Giemsa and examined for blood parasites. The external surface, fins, operculum, buccal cavity and all gill arches were examined thoroughly with a stereoscope. The content of the eyes and scrapings from the external surface and from slices of fins and two gill arches from each side of the fish were examined with a dissecting microscope. The body cavity was opened and searched for helminths with the naked eye as well as a stereoscope. Samples from all major organs (heart, brain, cranium, spinal cord, liver, kidney, spleen, gall bladder, urinary bladder, swim bladder, muscles and gonads) were examined for at least 5 minutes each, using both a stereoscope and a dissecting microscope. The alimentary tract was removed, cut longitudinally and scrapings prepared and searched for microparasites, using a microscope at high magnification. Finally the contents of the pyloric caecae and the intestine were examined for intestinal helminths using a microscope. Freezing of 17 of 40 fish prior to examination made detection of mobile internal micro-parasites, in this case Spironucleus (Hexamita) salmonis, impractical and hence no prevalence figures were given for that species.

All helminths found were counted and identified to species or genus level, and the prevalence and intensity (except for microparasites) of all species determined. The identification of species was based on Bykhovskaya-Pavlovskaya et al. (1964), Lom & Dyková (1992), Moravec (1994), El-Matbouli et al. (1999), Buchmann & Bresciani (2001), Gibson et al. (2002) and Jones et al. (2005). To aid identification, specimens of all species/ genera were photographed.

The conventional definitions of protozoa and myxozoa as microparasites and helminths and crustaceans as macroparasites were used. The definitions of ecological terms were according to Bush et al. (1997). Sörensen's index of similarity (qualitative measurements; values fall between 0 and 1) (Magurran 1988) was applied to measure similarities of the parasite fauna between localities and fish species.

RESULTS

Altogether at least 22 species of parasites were found collectively in arctic charr and brown trout from both lakes (Table 1).

Five protozoan species: Spironucleus salmonis n. comb. (formerly Octomitus salmonis sensu Moore, Davis, and Hexamita salmonis sensu Ferguson), Apiosoma sp., Capriniana piscium (Buetschli) Jankovski, Trichodina sp. and Dermocystidium branchiale Léger. Six myxozoan species: Chloromyxum truttae Léger, Myxidium truttae Léger, Myxobolus arcticus Pugachev & Khokhlov, Myxobolus cerebralis (Hofer), Myxobolus neurobius (Schuberg & Schroder) and Sphaerospora truttae Fischer-Scherl, El-Matbouli & Hoffmann. Nine helminth species: Apatemon gracilis (Rudolphi) Szidat, *Diplostomum* sp. (larvae), Crepidostomum farionis (O.F. Müller), Phyllodistomum conostomum (Olsson), Diphyllobothrium sp. (larvae), Eubothrium crassum

Table 1. Infected organs, number of infected fish, mean intensity and intensity range of the parasite species found in arctic charr and brown trout at each location.

		Elliðavatn (EV)					Hafravatn (HV)						
			rctic cha			rown tro		A	Arctic cha			rown tro	
Length range (cm)			25.0-39.0	25.0-39.0		28.5-38.0		19.0-26.5		5	13.5.33.0		
Age of fish (years)		3 - 7+		4+ -7+		3+ - 7		2 -7					
Number of fish examined			10			10			10			10	
			Intensity		Intensity		Intensity		nsity	Intensity			
	Infected organs	No. of inf. fish	Range	Mean	No. of inf. fish	Range	Mean	No. of inf. fish	Range	Mean	No. of inf. Fish	Range	Mean
Protozoa													
Spironucleus salmonis	IN/GB	+			+			+			-		
Apiosoma sp.	SK/GI	0			0			0			3		
Capriniana piscium	GI	4			1			1			7		
Trichodina sp.	SK	+			+			+			-		
Dermocystidium branchiale*	GI	5			2			0			2		
Myxozoa													-
Chloromyxum truttae*	GB	2			4			0			2		
Myxidium truttae*	IN/GB	0			1			0			0		
Myxobolus arcticus*	BR/SC	3			0			10			0		
Myxobolus cerebralis	BR	1			0			8			0		
Myxobolus neurobius*	BR/SP	0			2			0			2		
Sphaerospora truttae*	KI	0			0			0			1		
Helminths													
Apatemon gracilis	EY	0	0	0	0	0	0	0	0	0	2	1-2	1.5
Diplostomum sp. (larvae)	EY	10	148-808	432.5	10	11-140	44.5	10	224-1509	722.7	10	2-56	21.3
Crepidostomum farionis	IN	6	1-48	10.3	9	1-37	13.4	5	3-87	24.0	4	1-38	11.8
Phyllodistomum conostomum	KI	10	4-85	20.4	5	1-5	2.4	10	4-86	26.7	4	4-14	10.0
Diphyllobothrium sp. (larvae)	BC	1	1	1	2	1	1.0	10	12-46	24.5	9	1-21	6.1
Eubothrium crassum	IN	0	0	0	0	0	0	0	0	0	7	1-14	4.1
Eubothrium salvelini	IN	7	1-10	5.7	0	0	0	4	1-11	4.6	0	0	0
Philonema oncorhynchi	BC	0	0	0	0	0	0	7	1-22	8.7	0	0	0
Capillaria salvelini	IN	6	1-37	11.0	7	4-12	6.7	5	8-14	7.2	9	2-15	6.4
Crustacea													
Salmincola edwardsii	GI	3	2-8	5.0	0	0	0	0	0	0	0	0	0
Salmincola (salmonea) sp.	GI	0	0	0	1	1	1	0	0	0	0	0	0

Abbreviations: BC = body cavity, BR = brain, EY = eye, FI = fins, GB = gall bladder, GI = gills, IN = intestine, KI = kidney, SK = skin, SP = spinal cord. * = New parasite records for Iceland, + = found in one or more fish, - = not found

(Bloch), Eubothrium salvelini Schrank, Philonema oncorhynchi Kuitunen-Ekbaum and Capillaria salvelini Polyanskii. Two crustacean species: Salmincola edwardsii (Olsson) and Salmincola (salmonea (L.)) sp.

The overall similarity of the parasite fauna between the two lakes calculated as Sörensen's index was 0.78. Comparing the same fish species of the two lakes, the similarity of the total parasite fauna was 0.85 and 0.69 for arctic charr and brown trout, respectively (Table 2). In EV 17 species were found: 14 species in/on

Table 2. Similarity of micro- and macroparasites observed in the two lakes EV and HV (Sörenson's similarity index).

EV/HV-all species	0.78
EV/HV-micro-parasites	0.84
EV/HV-macro-parasites	0.71
EV/HV-charr-all species	0.85
EV/HV-trout-all species	0.69

arctic charr and 13 species in/on brown trout, with 10 species infecting both fish species. In HV 19 species were found: 12 species in/on arctic charr and 13 in/on brown trout, 6 species infecting both fish species. Fourteen species were found in both lakes.

The overall similarity of the microparasite fauna between the two lakes was 0.84 (Table 2). Comparing fish species and locations, the similarity ranged from 0.18-0.83, being highest for EV/HV charr, slightly lower for EV trout/EV charr and EV/HV trout, but notably lowest for HV trout/HV charr (Table 3.). Of the 11 microparasite species, 9 were found in EV and 10 in HV. Eight of the species were found in both lakes, 6 in or on both fish species, but no species was found in or on both fish species in both lakes. The prevalence of individual microparasite species did not differ markedly between lakes, except

for Myxobolus arcticus and M. cerebralis which were more commonly found in arctic charr in HV than in EV.

The overall similarity of the macroparasite fauna between the two lakes was 0.71 (Table 2). Comparing fish species and locations, the level of similarity ranged from 0.71-0.86, being lowest for EV trout/HV charr and HV trout/EV charr, slightly higher for EV trout/EV charr, EV/HV trout and EV trout/HV charr but highest for HV/EV trout and HV/EV charr (Table 3). Of the 11 macroparasite species 8 were found in EV and 9 in HV. Five of the 11 macroparasite species found were present in/on both fish spe-

No clear differences between sampling times (spring and autumn) were detected in the prevalence or intensity of the parasites and no relationship was evident between the age of the fish and their parasite burden.

DISCUSSION

The present study

cies in both lakes.

All 22 parasite species found in this study have previously been reported from arctic charr and brown trout in other countries. All the macroparasite species have been recorded from salmonids in Iceland before, but 6 of the 11 microparasites, i.e. Chloromyxum truttae, Myxidium truttae, Myxobolus arcticus, M. neurobius, Spaerospora truttae and Dermocystidium branchiale, are new parasite records in Icelandic fresh water. Only one further species has been reported from wild resident charr or trout in Iceland, i. e. Proteocephalus longicollis from charr (Frandsen et al. 1989). With the exception of Apiosoma sp. and Capriniana piscium, which infect a wide range of hosts, all the microparasites found are specific to salmonids. Regarding Trichodina species, many of which are generalists, they were not identified to a species level in this study. All the myxozoan- and macroparasite species found, except Apatemon gracilis, Diplostomum sp. and Diphyllobothrium sp., are restricted to salmonids.

The total parasite fauna of EV and HV

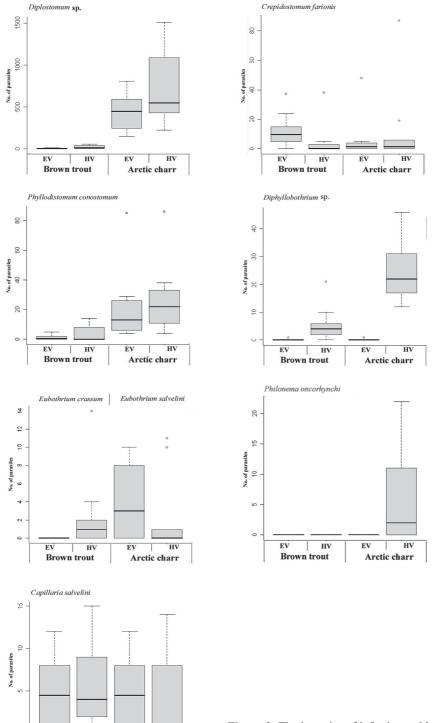
Table 3. Similarity between fish species and localities (Sörenson's similarity index). Above the diagonal = microparasites; below = macroparasites.

	EV trout	EV charr	HV trout	HV charr
EV trout		0.71	0.62	0.50
EV charr	0.77		0.46	0.83
HV trout	0.77	0.71		0.18
HV charr	0.77	0.86	0.71	

showed considerable similarity, both with regard to microparasites and macroparasites (Sörenson index = 0.84 and 0.71, respectively) (Table 3). The majority of species (14) were found in both lakes and many (10) in/on both fish species (Table 1).

Due to the limited sample size, this study, first and foremost, gives an overview of the most common species parasitizing arctic charr and brown trout in these two Icelandic lakes. Nonetheless the results give some indication of the differences in the parasite community structure between fish species and locations (Table 1 and Figure 2). Some species, e.g. Apiosoma sp., Myxidium truttae, Sphaerospora truttae, Apatemon gracilis, Salmincola edwardsii and Salmincola (salmonea) sp., only found in one of the lakes and/or fish species, had low prevalence and differences in their prevalence were most likely due to the limited sample size.

In some cases, different susceptibility of the hosts to certain parasite species accounts for variation in parasite fauna between fish species. Myxobolus cerebralis, which was only found in arctic charr in this study, is known to infect a wide range of salmonid species. Susceptibility to this infection, however, varies greatly between species, with brown trout considered more resistant to M. cerebralis than arctic charr (O'Grodnick 1979, El-Matbouli et al. 1999), which could explain why it was not found in brown trout. M. arcticus and M. neurobius have been reported from both arctic charr and brown trout (e.g. Sterud 1999). In our study, these species seemed to show host specificity, with M. arcticus only found in arctic charr and M. neurobius in brown trout. Myxobolus arcticus and M. cerebralis were noticeably more prevalent in charr from HV



HV

Arctic charr

EV HV Brown trout

Figure 2. The intensity of infections with the most common macroparasites found in arctic charr and brown trout from EV and HV.

than EV. Regarding M. cerebralis, susceptibility to this parasite not only varies among species but also among strains of the same species and even individual fish within a population (Markiw 1992). This could be one of the explanations for the difference in prevalence observed between the lakes. Eubothrium salvelini and S. edwardsii are considered specific to arctic charr (Kennedy 1977, Scholz et al. 2003). Philonema oncorhynchi is much more common in arctic charr and has not been found in brown trout in most studies (e.g. Hartvigsen & Halvorsen 1993, Dorucu et al. 1995, Byrne et al. 1999, Byrne et al. 2002). Brown trout is considered an unsuitable host for this species (Knudsen et al. 2007). Eubothrium crassum and S. salmonea are conversely more or less restricted to brown trout and salmon (Kennedy 1977, Scholz et al. 2003).

The digenean species Diplostomum sp. was found in all fishes examined from both lakes. However, the intensity of infections was much higher in arctic charr than brown trout in both lakes (Table 1 and Figure 2). The intermediate hosts for Diplostomum sp. are gastropods of the genus Radix (syn. Lymnea). Fish become infected by swimming cerariae released from the molluscs but possibly also via diet. Several reasons for this difference between these two fish species are conceivable. Brown trout could be more resistant to this infection, there could be some difference in the selection of habitat between the fish species making arctic charr more prone to exposure of swimming cercariae or difference in diet could be a factor.

A similar difference was observed for the digenea Phyllodistomum conostomum, the brown trout in the present study of both lakes being less infected than the arctic charr. These results are in accordance with studies from 1987-1999, where 20% of 480 arctic charr in EV were infected with P. conostomum but none of 480 brown trout (Antonsson & Gudbergsson 2000). However these prevalence values were much lower than in the present study (Table 1). Apparently, the life cycle of P. conostomum is not yet fully understood. Pisidium spp. and Sphaerium spp. are known

to serve as 1st intermediate hosts but the 2nd intermediate host is uncertain and may be lacking (Bakke 1985, Rahkonen & Valtonen 1987). Being the only freshwater bivalves in Icelandic fresh water, Pisidium spp. must serve as 1st (and possibly the only) intermediate hosts for this species in Iceland. If Pisidium species are the only intermediate host, possible explanations for this difference would be the same as given earlier for Diplostomum sp. If a 2nd intermediate host exists, a difference in diet would almost certainly be the reason.

Known intermediate hosts for Crepidostomum farionis are bivalves of the genera Pisidium and Sphaerium (1st intermediate hosts) and amphipods and ephemeroptera (2nd intermediate hosts) (Thomas 1958). In Icelandic fresh water Pisidium spp. are widespread (Hallgrímsson 1990) but Sphaerium spp. are apparently absent. Only two subterranean species of amphipods have been found in Iceland (Kristjánsson & Svavarsson 2007) and only one, somewhat rare, species of ephemeroptera (Cloëon simile, syn. C. praetextum (Tuxen)). Still, C. farionis was common, and in similar numbers, in both fish species in both lakes (Table 1 and Figure 2). Therefore some other species possibly serves as a 2nd intermediate host in these lakes or a 2nd intermediate host might not be needed.

The cestode species found in this study, i.e. Eubothrium crassum, E. salvelini and Diphyllobothrium sp., and the nematode species Philonema onchorhyncii are exclusively transmitted via diet. Fish become infected by ingesting copepods (primarily Cyclops spp.) or infected fish such as three-spined sticklebacks, a known reservoir host for Diphyllobothrium spp., and probably also Eubothrium spp. (Vik 1963, Vik 1964, Lien & Borgström 1973, Smith 1973, Henricson 1978, Bérubé & Curtis 1986). Three of the above-mentioned parasite species transmitted by copepods, i.e. Diphyllobothrium sp., Eubothrium crassum and Philonema onchorhyncii, seem clearly more common in HV than EV (Table 1 and Figure 2). In contrast the fourth species using copepods, Eubothrium salvelini, seems to be more

common in EV than HV (Table 1 and Figure 3). Furthermore Diphyllobothrium sp., the only species of the four that infects both fish species, was much more common in arctic charr than in brown trout.

Differences in the prevalence and/or intensity of parasite species transmitted through the diet often reflect differences in the selection of food eaten, even years back. There is information for EV concerning the availability of food for fish in the lake on a monthly basis during the period 1975-76 (Haraldsson 2004) and the food intake of arctic charr and brown trout during the period 1974-76 (Björnsson 2001, Björnsson 2002), also on a monthly basis. Furthermore, information on food intake of arctic charr and brown trout in EV in Sept./Oct. 1988-1999 during (Antonson & Gudbergsson 2000) and in both lakes in Sept./Oct. 2005 (Bjarnadóttir 2007) is available. These studies combined show that the availability of prey species, and hence the composition of food intake of both fish species, varies greatly within a year and between years.

Previous data from EV suggest considerable variation between years in prevalence of macroparasite species transmitted via diet. During 1974-76, 16% of the arctic charr (n = 961) and 81% of the brown trout (n = 429) were infected with Diphyllobothrium (Björnsson 2002) compared to 3% and 5% of arctic charr and brown trout (n = 480 for each fish species) respectively during 1987-1999 (Antonsson & Gudbergsson 2000). The results from the present study is in better accordance with the data from 1974-76 (Table 1). Similarly, the prevalence of Eubothrium spp. was 88% in arctic charr (n=961) and 5% in brown trout (n=429) during 1974-6 (Björnsson 2002) compared to 17% and 2% in arctic charr and brown trout (n = 480 for each fish species) respectively during 1987-1999 (Antonsson & Gudbergsson 2000). The results from the present study are in better accordance with the data from 1974-76 (Table 1).

The life cycle of Capillaria salvelini is not known (Moravec 1994). Its intensity in this study was similar in both fish species and both lakes (Table 1).

Although only found in EV in the present study (Table 1), Salmincola spp. infections in fish in HV have earlier been quite prevalent (Richter, unpublished data). In EV, during 1974-76, 41% of arctic charr and 23% of brown trout were infected with Salmincola (Björnsson 2002), whereas in 1987-1999 the prevalence of infection was only 9% in the arctic charr and 4% in the brown trout examined (Antonsson & Gudbergsson 2000).

Comparision to other lakes in Iceland

Earlier systematic quantitative studies on macroparasites and certain microparasite species of arctic charr and brown trout in Iceland exist from Lake Selvatn (SV) (Stefánsson, 1986) and of arctic charr in Lake Thingvallavatn (TV) (Malmquist et al. 1986, Frandsen et al. 1989, Jónsson & Gudbergsson 2003). In SV, a small but deep lake, connected downstream by a river with EV, 10 charr and 10 trout were examined for the presence of macroparasites, ectoparasitic protozoans and Spironucleus salmonis. In TV, in SW Iceland and the country's largest lake, 1299 fish of the 4 sympatric charr morphs present in the lake were examined for Diphyllobothrium sp. (Malmquist et al. 1986) and later 131 charr of the four morphs in the lake were examined for endoparasitic helminths (Frandsen et al. 1989). In addition, Jónsson and Gudbergsson (2003) examined 200 charr for larger helminths and Salmincola sp. No reports exist concerning parasites of brown trout in TV. With few exceptions, the parasite fauna in lakes HV and EV were in good agreement with the faunas observed in the lakes SV and TV. Some differences however could be detected.

An interesting difference was that Phyllodistomum conostomum has not been found in arctic charr in TV but has been found infecting every single charr and several trout examined in lakes HV and EV (Table 1) and the majority of charr from SV (Stefánsson 1986). This finding is especially interesting bearing in mind that the sample size in the studies of fish in TV

was far greater than in the other studies. This parasite must either have a very low prevalence in TV or be totally absent. As mentioned, Pisidium species are known to serve as 1st intermediate hosts for P. conostomum and Crepidostomum farionis. A 2nd intermediate host for P. conostomum is uncertain and may be lacking (Bakke 1985, Rahkonen & Valtonen 1987). Pisidium lilljeborgi (Esmark & Hoyer) is present, and P. casertanum (Poli) is common in TV (Lindegaard 1992) and numerous enough in TV to sustain Crepidostomum farionis in the lake (Frandsen et al. 1989). If these bivalves are sufficient as intermediate hosts for P. conostomum, a basis would be expected for the existence of this parasite in the lake. On the other hand, if a 2nd intermed-iate host is needed, an explanation of the seeming absence of P. conostomum in TV could be that this 2nd intermediate host is absent or exists in only very low numbers.

Another interesting difference between lakes in Iceland regards the cestode Proteocephalus longicollis. This species is common in TV charr, its prevalence ranging from 23 to 86%, depending on the charr morphs (Frandsen et al. 1989), but has not been found in EV, HV and SV. The life cycle of this parasite species is similar to that of Eubothrium spp. and Philonema oncorhynchi, cyclopoid (e.g. Cyclops spp.) and diaptomid copepods being the only known intermediate hosts (Hanzelová & Gerdeaux 2003). Cyclopoids and diaptomids are widespread in Icelandic fresh water (Hallgrímsson 1990) and present at least in Lake EV (Malm-quist et al. 2004) and most likely also in HV, i.e. intermediate hosts are available.

Patchiness in the distribution of certain parasite species has been reported from other studies in Iceland (Kristmundsson & Helgason 2007) and from abroad (e.g. Kennedy 1977, Hartvigsen & Halvorsen 1993). Kennedy (1977) examined parasites of arctic charr in Northern Norway and showed the absence of certain parasite species commonly infecting arctic charr (e.g. all acanthocephalans), although necessary intermediate hosts were abundant in these lakes. No explanation was given. Similarly, Hartvigsen & Halvorsen (1993), who studied brown trout in four lakes in Norway, found E. crassum in 76.7% of brown trout in one lake while no fish studied in the other three lakes was infected. Kristmundsson & Helgason (2007) observed similar differences in the parasite faunas of eels from several lakes in Iceland. All necessary intermediate hosts were present in all lakes, although some parasite species which were common in one lake were not found in the other lakes. They stated that this could to some extent be explained by the different composition of the fish fauna of the lakes as well as a dissimilar choice of prey related to difference in eel size.

Surveys made of the fish populations of EV and HV indicate strong trends towards the fish in EV growing faster than in HV. Consequently, both arctic charr and brown trout in EV seem to be larger than in HV in comparison to age. This seems especially apparent for the arctic charr (Antonsson & Gudbergsson 2000, Bjarnadóttir 2007). The length-age relationship of the fish caught in this study showed the same trend (Figure 1). It is well known that fish populations of distinct lakes evolve differently with regards to both morphology and growth rate. Many factors can influence the evolution of a certain population of fish. The lakes EV and HV are similar in area, but quite different in other respects such as depth and water volume. Consequently, they afford quite different ecosystems for their inhabitants. Living conditions, e.g. food availability and food specialisation, are without doubt influential factors. Diseases, among them parasites, can also affect growth rate. Infections of some parasite species in this study, e.g. Diphyllobothrium sp., Philonema oncorhynchi and Eubothrium crassum, seemed clearly more intense in HV than EV. Parasites could therefore have been among the factors causing the observed differences in growth rates in HV and EV.

Comparision to neighbouring countries

Arctic charr is a northern species. Areas from which data on the parasite fauna of arctic charr are available include Greenland (Due & Curtis 1995), Jan Mayen (Kennedy 1977), Spitzbergen (Kennedy 1977, Sobecka & Piasecki 1993, Hammar 2000), Bear Island (Kennedy 1978), the mainland of Norway (e.g. Kennedy 1977, Knudsen et al. 1997, Sterud 1999, Knudsen et al. 2007) and the British Isles (e.g. Kennedy 1974, Holland & Kennedy 1997). Brown trout has a more southern distribution and is not present on arctic islands such as Jan Mayen, Spitzbergen and Bear Island. Parasites of brown trout have been extensively studied in Norway and the British Isles (e.g. Kennedy 1974, Hartvigsen & Halvorsen 1993, Hartvigsen & Kennedy 1993, Molloy et al. 1993, Dorucu et al. 1995, Molloy et al. 1995, Byrne et al. 1999, Sterud 1999, Kennedy & Hartvigsen 2000, Byrne et al. 2002, Byrne et al. 2003, Knudsen et al. 2007).

The number of observed parasite species reflects the species richness in the ecosystem in the lakes. During the last glaciation the northern hemisphere, including Iceland, was mostly ice covered. For that reason, most of the species of the present fauna have colonized this area during the last 8 to 10 thousand years. The richness of the present fauna is affected by the environment, opportunity and time span for new species to colonize these areas. The geographical location and climate of Iceland and other isolated northern islands have certainly hampered this re-colonization. Microparasites have not been found on Spitzbergen, Bear Island, Jan Mayen (Kennedy 1977, Kennedy 1978) and Greenland (Due & Curtis 1995).

Odonata, ephemeroptera and freshwater amphipoda and mysidea have not been found in Jan Mayen, Spitzbergen, Bear Island and Greenland (Kennedy 1978, Røen 1975) and in Iceland only subterranean species of amphipods and one, somewhat rare, species of ephemeroptera have been found. Furthermore, freshwater molluscs have not been found in Jan Mayen, Spitzbergen and Bear Island but they are present in Greenland (Røen 1981) and common in Iceland (Hallgrímsson 1990). As these groups serve as intermediate hosts for many common macroparasites of salmonids, their absence, rareness or limited distribution greatly limit the diversity of the parasite fauna in these areas. Due to the absence or low intensity of odonata, ephemeroptera and freshwater amphipoda and mysidea, salmonids in Iceland and the arctic charr in Greenland, Jan Mayen, Spitzbergen and Bear Island seem to lack acanthocephalans and several other parasites which use these species as intermediate hosts, but such parasites are common in arctic charr in Norway and the British Isles. Apart from the apparent absence of Phyllodistomum farionis and Capillaria salvelini in Greenland (Due & Curtis 1995), parasites which are very common in Iceland, the macroparasite fauna of arctic charr in Greenland and Iceland seem to be quite similar. The main difference in the macroparasite fauna between Iceland on one side and Spitzbergen and Bear Island on the other is the total lack of digenean species on the latter two islands, which can be explained by the absence of all freshwater molluscs (Kennedy 1978). The arctic charr in Jan Mayen seem to be completely free of parasites (Kennedy 1977), which definitely is due to the extreme poverty of the invertebrate fauna (Skreslet & Foged 1970).

All the parasites found on and in arctic charr in Iceland have also been found in Norway, and all the parasites found on and in brown trout in Iceland have also been found in Norway and the British Isles. Many of the most common parasite species of arctic charr elsewhere, e.g. in Norway, and of brown trout elsewhere, e.g. in Norway and the British Isles (e.g. Hartvigsen & Halvorsen 1993, Hartvigsen & Kennedy 1993), have also been found in Iceland.

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