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RESEARCH ARTICLE

Occurrence and seasonality of *Gyrodactylus salaris* and *G. salmonis* (Monogenea) on Arctic char (*Salvelinus alpinus* (L.)) in the Fustvatnet lake, Northern Norway

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Abstract

Gyrodactylus spp. (Monogenea) were found on 16.9% (233 out of 1376) Arctic char, *Salvelinus alpinus* (L.), sampled from September 2010 to October 2011 in the Fustvatnet lake, Northern Norway. Two species were identified: *G. salaris* Malmberg, 1957, and *G. salmonis* Yin & Sproston, 1948. *Gyrodactylus salaris* was only found on Arctic char larger than 28 cm and only in samples obtained in the autumn (September and October). *Gyrodactylus salmonis* was found on Arctic char of all sizes (11–47 cm) and throughout the year, with a small peak in abundance in the late autumn (November). *Gyrodactylus salaris* was found to prefer the tail and dorsal fin. Based on the results, we recommend that surveys of Arctic char for the presence of *G. salaris* are based on the examination of the fins of large fish sampled during the spawning season (autumn).

KEYWORDS
ectoparasites, monitoring, salmonids, seasonal abundance, site distribution

1 | INTRODUCTION

The introduced monogenean parasite *Gyrodactylus salaris* Malmberg, 1957 has had devastating effects on Atlantic salmon, *Salmo salar* L., populations in Norwegian rivers since its first introduction more than 40 years ago (Johnsen, 1978; Johnsen & Jensen, 1991, 2003). Until today, *G. salaris* has been detected in 51 Norwegian rivers (Hytterød et al., 2020). To reduce the risk for further spread to additional rivers and to restore the Atlantic salmon populations in the affected rivers, the Norwegian government has decided to eradicate *G. salaris* from all affected rivers (Anonymous, 2014). This has been done by carrying out chemical eradication measures, mainly using rotenone, a pesticide that kills all the fish host and thus also *G. salaris* (Anonymous, 2014).

During the preparations for chemical treatment of ten salmon rivers in or near the Vefsn Fjord in Nordland County, Northern Norway, it was established that *G. salaris* was also present on resident Arctic char, *Salvelinus alpinus* (L.), in three lakes in the region: Fustvatnet, Mjåvatnet and Ømmervatnet (Hytterød et al., 2011). These lakes are draining into the Fusta river, one of the infected rivers that were to be treated. The natural migration of salmon (*Salmo salar*) to these lakes came to a halt when the fishing ladder in the Fusta river was closed in 1992 (Sæter, 1995), and the salmon have probably been absent in the lakes ever since. It is thus likely that *G. salaris* has been present in the char population since at least 1992 and because of this presence, the three lakes were included in the synchronous chemical treatment of all the rivers in and near the Vefsn Fjord (Stensli & Bardal, 2014).

Previous studies have shown that Arctic char can be a long-term host for *G. salaris*, both in Arctic char populations living in rivers in Northern Norway (Winger et al., 2009) and in lakes in Southern Norway (Robertsen et al., 2007). Several different strains

(haplotypes) of *G. salaris* have been observed in Norway (Hansen et al., 2003), and three of these have now been found on char. The strain found on river-living Arctic char in Northern Norway (haplotype B) (Winger et al., 2009) is pathogenic to Atlantic salmon, while the strain found on lake-living Arctic char is in Southern Norway (haplotype F), is non-pathogenic (Olstad et al., 2007). The variant found on char in the lakes Fustvatnet, Mjåvatnet and Ømmervatnet (Hytterød et al., 2011), and which is studied here, is the haplotype A, a pathogenic variant that is by far the most common haplotype affecting Atlantic salmon in Norwegian rivers (Hansen et al., 2003).

After chemical treatments of lakes and rivers in Norway, the absence of *G. salaris* must be documented before the watercourse can be declared free from the parasite. Normally this is done by examination of Atlantic salmon parr from previously infected rivers for 5 years following eradication (see e.g. Hansen et al., 2022). As *G. salaris* in this case was not found on its main host, knowledge on the prevalence, abundance and site specificity of the parasite on this host is important knowledge to optimize the detection of the parasite following the eradication. In addition, this knowledge is also of importance for the detection of *G. salaris* on Arctic char in other affected watercourses.

Earlier studies have shown a seasonal and host age-dependent occurrence of both the haplotypes B and F of *G. salaris* in Arctic char (Robertsen et al., 2008; Winger et al., 2007). Furthermore, it is known that *G. salaris* prefers dorsal and pectoral fins in Atlantic salmon (Appleby & Mo, 1997; Jensen & Johnsen, 1992; Mo, 1992) while similar studies have not been done for *G. salaris* on Arctic char. Thus, we initiated a study on seasonal variation in abundance, site distribution and host age-dependent presence of *G. salaris* haplotype A on Arctic char in the Fustvatnet lake. In the initial examinations, we found that Arctic char in the lake were also infected with *G. salmonis* Yin & Sproston, 1948 (see Leis et al., 2021). Thus, both *Gyrodactylus* species were included in the study.

2 | MATERIALS AND METHODS

2.1 | Sampling locality

Lake Fustvatnet (65°54′23.0″N 13°23′37.0″ E), Nordland County, Northern Norway, is located 39 meters above sea level and covers 10.6 km^2. The mean depth is 21 m, and the maximum depth is 65 meters. Fustvatnet is usually ice-covered from October/November to May next year. The fish fauna consists of Arctic char (hereafter referred to as char), brown trout (*Salmo trutta* L.) and three-spined stickleback (*Gasterosteus aculeatus* L.), while the European eel (*Anguilla anguilla* (L.)) is rare in the system. As mentioned in the introduction, anadromous populations of Atlantic salmon, in addition to sea running brown trout, could earlier enter the lake via a fish ladder in the Fusta river, but this ladder was closed in 1992 and the anadromous salmonids disappeared in all three lakes upstream (Sæter, 1995).

2.2 | Fish sampling

Char were caught alive in one large and several small traps during eight 10-day periods from September 2010 to October 2011 (Table 1). During the ice-free period of the year, all the traps were operated from a boat. During the ice-covered period, the small traps were operated through holes cut in the ice, while the large trap was not used due to operational challenges. After being removed from the traps, the fish were killed before further processing. No approval from Institutional Animal Care and Use Committee (IACUC) or ethics committee was necessary. Based on previous experience, examining the whole body surface of fish larger than 22 cm under a stereo microscope is impractical and very time-consuming. In addition, the preservation of fish larger than 22 cm would require the use of unreasonable quantities of 96% EtOH for preservation (see below). Thus, only char smaller than 22 cm was preserved as whole fish in 96% EtOH. These fish were preserved in 2 litres of plastic bottles with five fish in each bottle. Char larger than 22 cm was weighed and the total length measured before all the fins (except the adipose fin) were cut off with a pair of scissors. Using a pair of tweezers, all fins from each char were transferred to a separate 500 ml plastic bottle with 96% EtOH and the bottle was labelled with date and fish number. The abdomen of the large char was cut open and the sex was determined in the field. The sex of the small char was determined in the laboratory after the examination of *Gyrodactylus* specimens.

2.3 | Fish examination

Whole small char (<22 cm) and fins from large char (>22 cm) were examined for the presence of *Gyrodactylus* specimens under a stereo microscope. The seven fins that were cut off the large char were identified as the left or right pectoral or pelvic fin, dorsal fin, anal fin and tail fin based on their shape and upper and lower coloration. The position of each *Gyrodactylus* specimen on the fish body and fins was noted and labelled with a unique fish and parasite number. Each *Gyrodactylus* specimen was removed from the host tissue with tiny watchmaker forceps and transferred to 96% EtOH in a 1.5 ml Eppendorf tube, each labelled with a unique number.

2.4 | Parasite identification

Individual parasite specimens were identified as species based on sequencing of the internal transcribed spacer 2 (ITS2) (~450 base pairs) of the ribosomal rRNA gene cluster. The use of the full ITS fragment (consisting of ITS1, 5.8 S and ITS2) is recommended by the World Organisation for Animal Health, WOAH, for diagnostics of *G. salaris*, but ITS2 alone can discriminate between *G. salaris* and *G. salmonis*. For the purpose of this study, ITS2 was therefore chosen because the shorter length of the fragment makes amplification easier and more consistent and no internal are necessary for

sequencing. Specimens of *G. salaris* were not characterized further to strain (mtDNA haplotypes), but based on previous results, all *G. salaris* specimens likely belonged to haplotype A. (see Hansen et al., 2003).

A note on names. Two *Gyrodactylus* species had been described from char in Eurasia prior to the start of this study; *G. birmani* Konovalov, 1967 from Kamchatka in the eastern part (Konovalov, 1967) and *G. salvelini* Kuusela, Ziętara & Lumme, 2008 from Finland in the western part (Kuusela et al., 2008). However, Leis et al. (2021), studied *G. salmonis*, a species described from several salmonids in North America (Cone et al., 1983; Yin & Sproston, 1948) and synonymized *G. salvelini* to *G. salmonis*, giving *G. salmonis* a circumpolar distribution in the northern hemisphere. Leis et al. (2021) did not consider the status of *G. birmani* and there are no DNA sequences in GenBank for this species to compare with. As the molecular comparison identifies the species as *G. salmonis*, we use this name here. This is the first time *G. salmonis* is reported from Norway.

DNA was extracted from each individual specimen using the DNEasyKit or Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The primer pair ITS4.5 and ITS2 (Matejusova et al., 2001) were used to amplify the ITS2 fragment. The PCR reactions were carried out with puRe Taq Ready-to-Go PCR beads (GE Healthcare) in a GeneAmp® PCR System 9700 (Applied Biosystems) following previously published PCR protocols for ITS2 (Matejusova et al., 2001). The PCR products were purified using a QIAquick PCR Purification Kit (Qiagen) or Macherey-Nagel NucleoSpin® Extract II according to the manufacturer's recommendations. DNA strands were sequenced using the PCR primers on an ABI 3700XL (Applied Biosystems) using DyeET-terminator mix (GE Healthcare). The sequences were proofread in VectorNTI 11.5. (Invitrogen) and aligned to ITS2 sequences from *G. salaris* and *G. salmonis* retrieved from NCBI GenBank to establish the species identity.

2.5 | Data and statistical analysis

Calculation and figures of seasonality and distribution of *Gyrodactylus* spp. on char were done in Microsoft Excel, and statistical tests and graphics were fitted in R v4.1.2 (R Core Team, 2022). General linear models (GLM) were fitted to explain the variation in the total number of *G. salaris* and *G. salmonis* (using a Poisson distribution) where fish length and sex were added as explanatory variables. Plots were fitted using ggplot2 (Wickham, 2016).

3 | RESULTS

3.1 | Parasite diagnostics and infection parameters

In total, 233 out of 1376 (16.9%) examined char were found infected with *Gyrodactylus* spp. (Table 1). A total of 884 *Gyrodactylus* specimens were recovered from these fish and of these, 839 *Gyrodactylus* specimens were identified as either *G. salaris* or *G. salmonis* using molecular methods. The DNA extraction or PCR analysis failed for 45 specimens and thus their species identity could not be established. Among these 45 unidentified *Gyrodactylus* specimens, 33 occurred on char smaller than 22 cm. As no *G. salaris* were present among the identified specimens from char of this size (see below), these 33 specimens were likely *G. salmonis*. A similar assumption could not be done for the twelve remaining unidentified *Gyrodactylus* specimens recovered from char larger than 22 cm, as some char of this size were infected with both *Gyrodactylus* species. Because of the uncertainties, we excluded all the 45 unidentified *Gyrodactylus* specimens from the calculations of occurrence and seasonality for *G. salaris* and *G. salmonis* separately but included them in the calculations involving the total numbers of *Gyrodactylus* spp. on char (Table 1; Figure 1).

In total, 172 *G. salaris* specimens were recovered from 40 char larger than 22 cm, all from fish sampled in September 2010, October 2010 and October 2011. No *G. salaris* were found on char in the other five samples (Table 1; Figure 2). When all char were included, the prevalence, mean intensity and abundance of *G. salaris* were 2.9%, 4.3 and 0.1, respectively. However, when only char larger than 22 cm are included in the calculations, the corresponding numbers are 8.9%, 4.3 and 0.4. The highest prevalence (19.0%) of *G. salaris* on char (>22 cm) was observed in September 2010. This month included the most infected char (male), which harboured at least 64 *G. salaris* specimens. As no *G. salmonis* were found on this fish, the two unidentified specimens were most likely also *G. salaris*.

Among the 40 infected large char, 20 were mature females, 18 were mature males while two char were immatures. Of the 166 *G. salaris* recovered from large char from which the sex was established, 56 parasites were from female fish ($n = 20$) and 110 parasites were from male fish ($n = 18$). A GLM of the total number of *G. salaris* on each fish showed that males had significantly more *G. salaris* than females (Table 2; Figure 4a). There was no interaction between length and sex for char ($z = -1.66$; $p = .10$).

Gyrodactylus salmonis occurred on char in all eight sample months (Table 1; Figure 3). The overall prevalence, mean intensity and abundance of *G. salmonis* were 13.9%, 3.5 and 0.5, respectively (Table 1). The highest prevalence (32.8%) of *G. salmonis* occurred in November 2010. The most highly infected char was sampled in October 2010, a fish harbouring at least 32 *G. salmonis* specimens. Five unidentified specimens were likely also *G. salmonis*, as *G. salaris* was not found on small char (<22 cm). A GLM of the total number of *G. salmonis* on each fish showed that males had significantly more *G. salmonis* than females (Table 2; Figure 4b). There was no interaction between length and sex for char ($z = 0.27$, $p = .79$).

3.2 | Site distribution

Ninety-two (53.5%) of the 172 *G. salaris* specimens infected the tail fin of large char while 52 (30.2%) specimens were found on the dorsal fin. The remaining *G. salaris* specimens occurred on the anal fin (6.4%), left pectoral fin (4.7%), right pectoral fin (3.5%) and the left pelvic fin (1.3%) (Figure 5a).

Among all the 667 identified *G. salmonis* specimens, 299 (44.8%) occurred on the dorsal fin. The remaining *G. salmonis* specimens

TABLE 1 Prevalence (in %), mean intensity, abundance, variation in parasite number and total parasite number of *Gyrodactylus* spp. *G. salaris* and *G. salmonis* on Arctic char in Lake Fustvatnet in the period September 2010 to October 2011

Month	September 2010	October 2010	November 2010	February 2011	April 2011	June 2011	September 2011	October 2011	Total
Number of char	153	208	177	116	169	191	188	174	1376
Gyrodactylus spp.									
Number infested	56	38	61	16	9	8	24	21	233
Prevalence (%)	36.6	18.3	34.5	13.8	5.3	4.2	12.8	12.1	16.9
Mean intensity	4.0	5.3	3.8	1.6	2.9	9.0	1.5	3.2	3.8
Abundance	1.5	1.0	1.3	0.2	0.2	0.4	0.2	0.4	0.6
Variation in Gyro no.	1–66	1–37	1–29	1–5	1–9	1–24	1–6	1–13	1–66
Total Gyro no.	226	202	229	26	26	72	35	68	884
G. salaris									
Number infested	29	8	0	0	0	0	0	3	40
Prevalence (%)	19.0	3.8	0	0	0	0	0	1.7	2.9
Mean intensity	4.8	3.5	0	0	0	0	0	2.0	4.3
Abundance	0.9	0.1	0	0	0	0	0	0.03	0.1
Variation in Gyro no.	1–64	1–15	0	0	0	0	0	1–4	1–64
Total Gyro no.	138	28	0	0	0	0	0	6	172
G. salmonis									
Number infested	31	31	58	16	9	8	21	17	191
Prevalence (%)	20.3	14.9	32.8	13.8	5.3	4.2	11.2	9.8	13.9
Mean intensity	2.7	5.2	3.7	1.5	2.9	8.9	1.5	3.4	3.5
Abundance	0.5	0.8	1.2	0.2	0.2	0.4	0.2	0.3	0.5
Variation in Gyro no.	1–16	1–37	1–29	1–5	1–9	1–24	1–5	1–12	1–37
Total Gyro no.	84	162	212	24	26	71	31	57	667

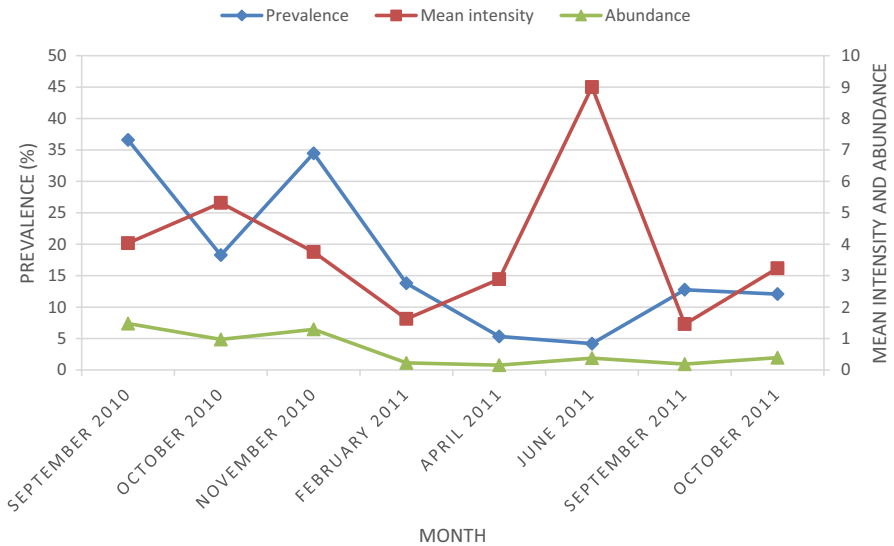

FIGURE 1 Seasonality in prevalence (in %), mean intensity and abundance of *Gyrodactylus* spp. on all Arctic char sizes in Lake Fustvatnet.

occurred on the body (13.0%), anal fin (12.1%), tail fin (10.2%), right pectoral fin (6.0%), left pectoral fin (3.6%), adipose fin (3.3%), right pelvic fin (2.7%), left pelvic fin (2.2%) and the head (1.3%) (Figure 5b). On char smaller than 22 cm, the 467 recorded specimens of *G. salmonis* had the following distribution: 240 (51.4%) occurred on the dorsal fin, while the remaining specimens were found on the body (18.6%), tail fin (6.4%), anal fin (5.4%), adipose fin (4.7%), right pectoral fin (3.2%), right pelvic fin (2.8%), left pectoral fin (2.4%), left pelvic fin (11) and the head (2.8%) (Figure 5b). On char larger than 22 cm, the distribution of the 200 recorded *G. salmonis* had the following distribution: Fifty-nine (29.5%) occurred on the dorsal fin while the remaining specimens were found on the anal fin (28.0%), tail fin

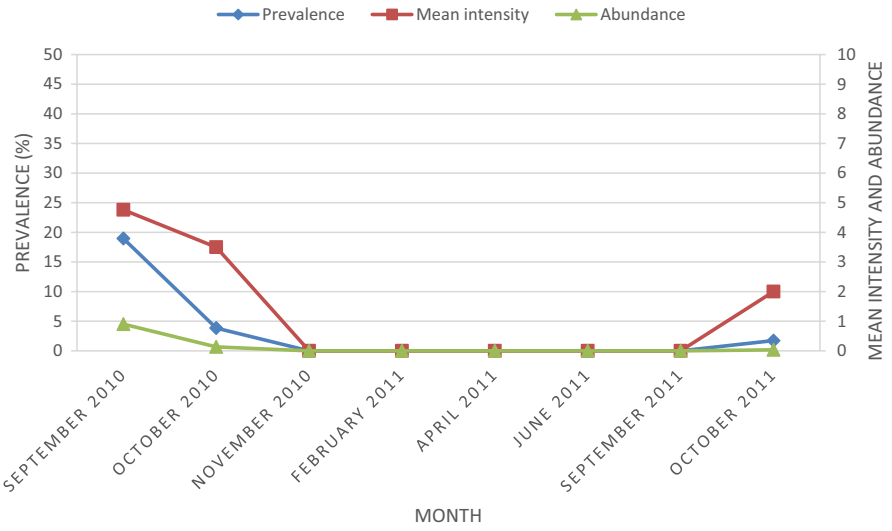

FIGURE 2 Seasonality in prevalence (in %), mean intensity and abundance of *Gyrodactylus salaris* on Arctic char (>22 cm) in Lake Fustvatnet.

TABLE 2 General linear model (GLM) of number of *G. salaris* and *G. salmonis* in relation to length and sex in Arctic char

	Estimate	SE	Z	*p*
G. salaris				
(Intercept)	0.11	0.47	0.23	.82
Length	0.00	0.00	2.03	.042
Sex (male)	0.70	0.17	4.10	<.001
G. salmonis				
(Intercept)	0.82	0.11	7.21	<.001
Length	0.00	0.00	0.66	.51
Sex (male)	0.66	0.09	7.74	<.001

Note: The number of parasites was fitted using a Poisson distribution.

(19.0%), right pectoral fin (12.5%), left pectoral fin (6.5%), right pelvic fin (2.5%) and left pelvic fin (2.0%) (Figure 5b).

Gyrodactylus salaris and *G. salmonis* occurred together on seven large char: five females and two males. In four of the females, the number of *G. salaris* was higher than the number of *G. salmonis*, while the opposite was observed for two male char. The last female was infected by one specimen of each *Gyrodactylus* species. On six fish, both *Gyrodactylus* species were recovered from the same fin, either on the dorsal fin, tail fin and left or right pectoral fin.

4 | DISCUSSION

Gyrodactylus salaris was only found on char larger than 28 cm and only in September 2010, October 2010 and October 2011. As only the fins of large char (>22 cm) were examined, *G. salaris* likely occurred on the body, head or gills in the five sampling periods between October 2010 and October 2011. Alternatively, the number of char examined was too low to detect the few *G. salaris* present on fins in these sampling periods. The increased abundance of *G. salaris* (haplotype A) in the autumn is consistent with previous observations of *G. salaris* (haplotype F) on char in lakes in Southern Norway (Robertsen et al., 2008) and *G. salaris* (haplotype B) on char in rivers in Northern Norway (Winger et al., 2007). The higher abundance of *G. salaris* on large and older char in Fustvatnet is also consistent with previous observations of *G. salaris* on mature char in lakes in Southern Norway (Robertsen et al., 2008). *Gyrodactylus salmonis* was present on char in all eight sampling periods and on all lengths of char (11–47 cm). The abundance was low throughout the year with a small peak in the late autumn (November).

The increased abundance of *Gyrodactylus* spp. in the autumn corresponds to the spawning period of the char in Fustvatnet and may reflect a reduced host immune response in this period. Evidence shows that the spawning process depresses immunity in fish (Krams et al., 2017), and this explains the peak in the abundance of some parasite infections during the spawning period (Koskivaara et al., 1991; Skarstein et al., 2001). In addition, a peak in parasite abundance during the host spawning period may also be an adaptation for transmission in the viviparous *Gyrodactylus* species because the hosts are in close contact in this period and thus there is an increased probability of transmission to a new host individual.

More than half of the *G. salaris* specimens were found on the tail fin and almost one-third on the dorsal fin of the large char. This is different from the site distribution in Atlantic salmon parr where most of the *G. salaris* specimens are found on the dorsal fin and the pectoral fins (Appleby & Mo, 1997; Jensen & Johnsen, 1992; Mo, 1992). However, Jensen and Johnsen (1992) observed that the proportion of *G. salaris* on the tail fin was higher when the total number of *G. salaris* was low (less than 100). As only the fins were examined and some *G. salaris* specimens probably occurred elsewhere on the char, the site distribution of *G. salaris* in adult char and Atlantic salmon parr is not completely comparable. However, it seems likely that most *G. salaris* specimens show a preference for the fins of char as they do in Atlantic salmon.

Even if both *G. salaris* and *G. salmonis* occurred on fins of char in the Fustvatnet lake, most of the infected char were either infected with *G. salaris* or with *G. salmonis*. Both *Gyrodactylus* species were

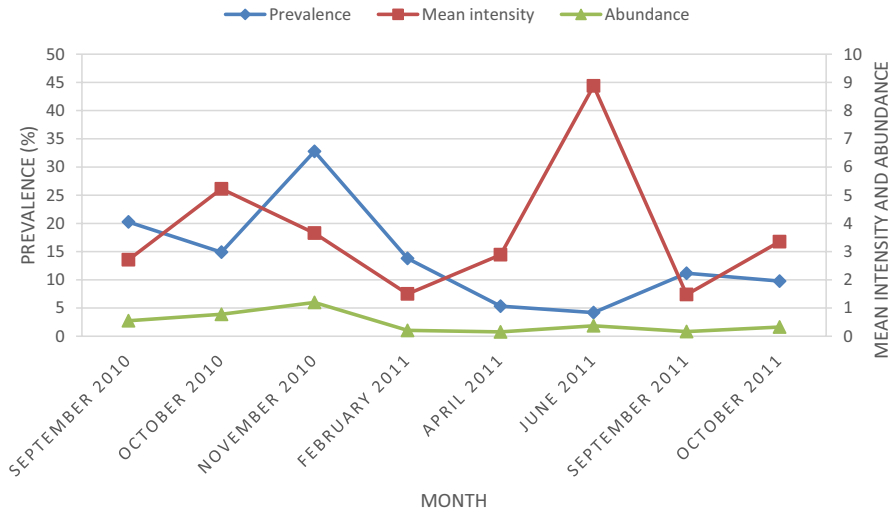

FIGURE 3 Seasonality in prevalence (in %), mean intensity and abundance of *Gyrodactylus salmonis* on all Arctic char sizes in Lake Fustvatnet.

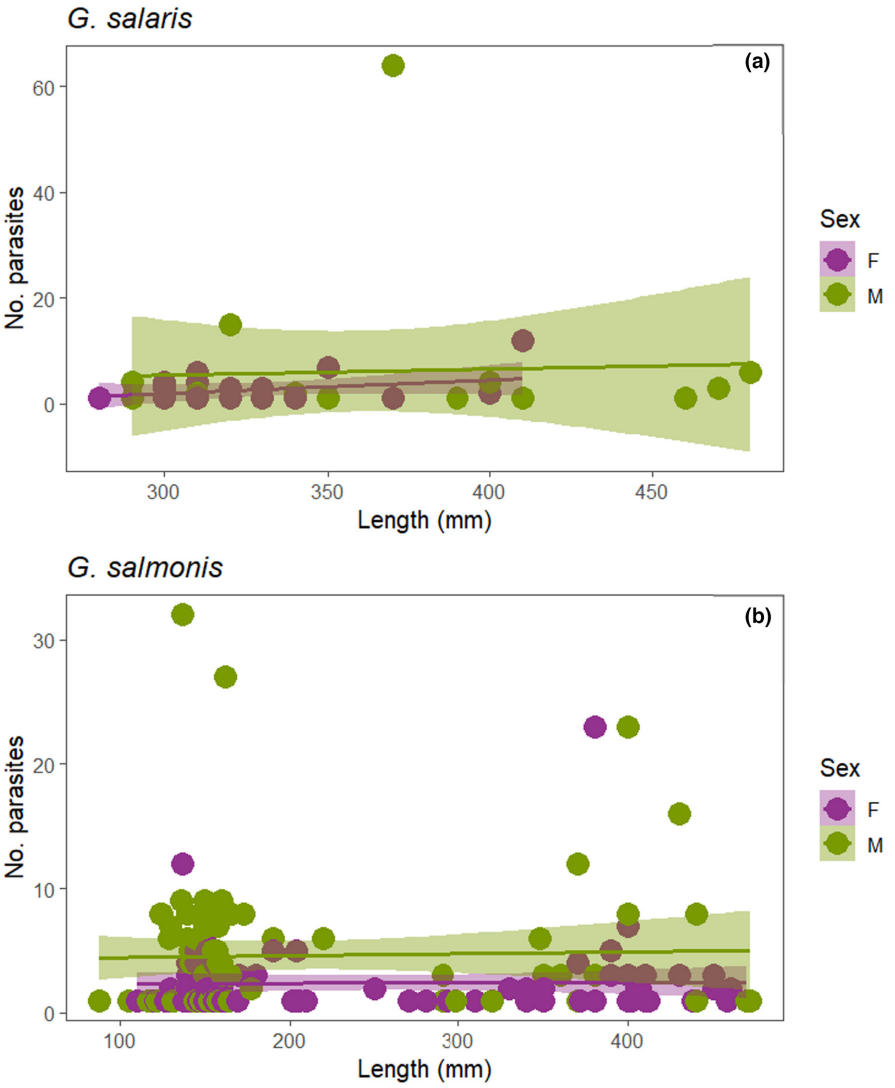

FIGURE 4 Occurrence of *G. salaris* and *G. salmonis* with length and sex of Arctic char in Lake Fustvatnet. (a) *G. salaris* on large char (>22 cm), (b) *G. salmonis* on all char sizes.

only found on the fins of seven large char (>22 cm), and in six of these, both parasite species occurred on the same fin. The rare occurrence of both *Gyrodactylus* species on the same char specimen could indicate an interspecific competition. Mutual exclusion of congeneric monogenean species has been observed if the space in the habitat offered by the host is limited (Jackson et al., 1998). However, as the number of *Gyrodactylus* specimens on each char was low and each parasite seemingly had plenty of space, we find unlikely that the low co-occurrence of *G. salaris* and *G. salmonis* was not due to interspecific competition.

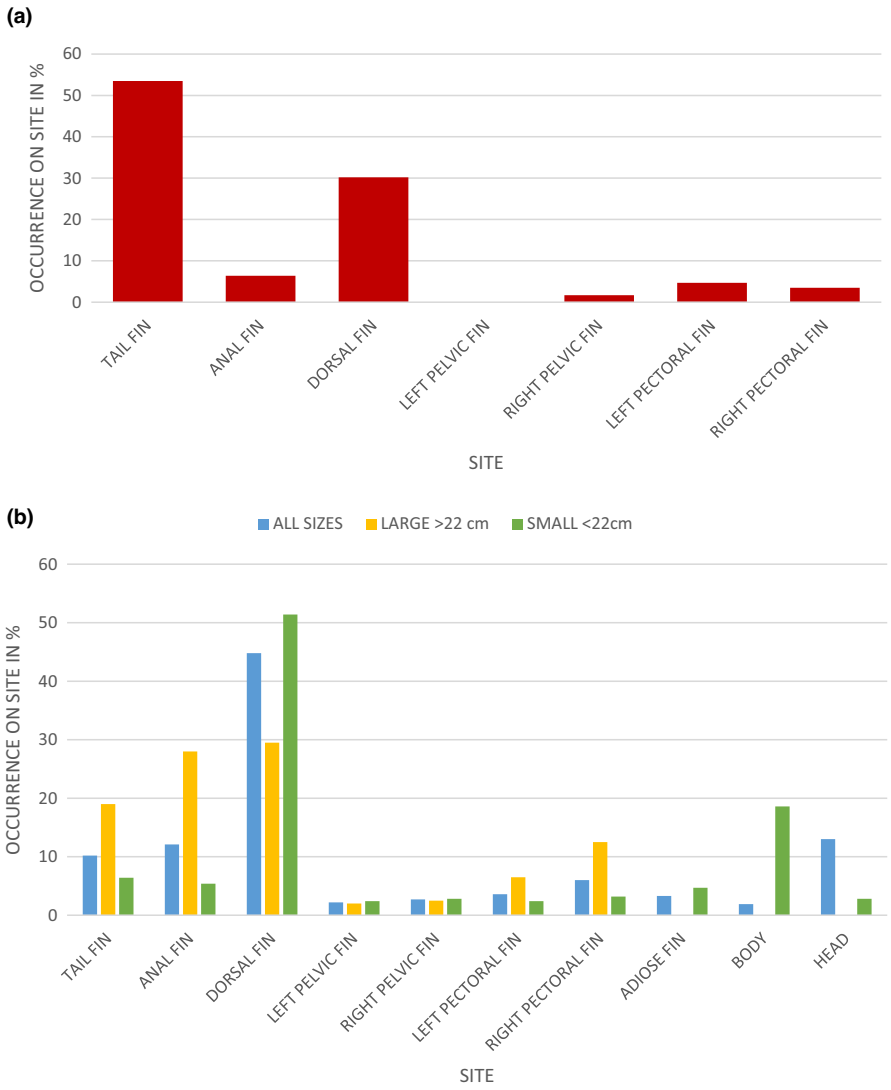

FIGURE 5 Site distribution of *G. salaris* and *G. salmonis* on Arctic char in Lake Fustvatnet. (a) *G. salaris* on large char (>22 cm), (b) *G. salmonis* on all sizes, large and small char, respectively.

In 2012, about 1 year after the completion of sampling for this study, the Fustvatnet lake, two other lakes and ten rivers in and near the Vefsn Fjord, were treated with the piscicide rotenone to eradicate all fish and *G. salaris*. Prior to the treatment, numerous mature char and brown trout were sampled in the lakes while mature Atlantic salmon and sea trout were sampled in the rivers. Stripped fish eggs were fertilized and grown in a hatchery and in the following years, yearlings and older fish, free from *G. salaris* (and *G. salmonis*), were stocked in the rivers and lakes to re-establish the fish populations with fish of local origin. Following treatments, the success of the eradication measures carried out in the rivers and lakes needs documentation. In the rivers, *G. salaris* infects mainly Atlantic salmon parr and these parr become numerous within a few years. These rivers are thus generally declared free from *G. salaris* after examination of a high number of parr for 5 years following treatment (Hansen et al., 2022). However, as it was found in this study that *G. salaris* on char occurs mostly or exclusively on mature fish larger than 22 cm, and that the prevalence and intensity are highest in autumn, the examination of fish larger than this size and sampled in late autumn is examined for *G. salaris* in the post-treatment surveillance programme (Hansen et al., 2022). The population of Artic char obviously took some years to recover to a size where a large enough number of char of suitable size could be obtained, and thus, the post-treatment surveillance programme for Arctic char did not start before 2021. Based on the low prevalence and intensity of *G. salaris* before treatment, 500 char are examined for the presence of *G. salaris* for 3 years before the lakes can be declared free from this parasite. Salmon parr from the Fusta river have been examined all years since treatment with no *G. salaris* detected. Thus, we see that the results from this study have already had management implications.

AUTHOR CONTRIBUTIONS

Tor Atle Mo involved in conceptualization (equal), formal analysis (lead), funding acquisition (equal), project administration (equal), investigation (equal), methodology (equal), writing—original draft (lead) and writing—review and editing (lead). **Sigurd Hytterød** involved in conceptualization (equal), funding acquisition (equal), project administration (equal), investigation (equal), methodology (equal) and writing—review and editing (equal). **Haakon Hansen** involved in conceptualization (equal), formal analysis (equal), funding

acquisition (equal), investigation (equal), methodology (equal) and writing—review and editing (equal).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data on char and parasite occurrence that were compiled in this project are presented in tables in the manuscript.

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