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Distribution and prevalence of the myxozoan parasite *Tetracapsuloides bryosalmonae* in northernmost Europe: analysis of three salmonid species

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ABSTRACT: Global climate change is altering the abundance and spread of many aquatic parasites and pathogens. Proliferative kidney disease (PKD) of salmonids caused by the myxozoan *Tetracapsuloides bryosalmonae* is one such emerging disorder, and its impact is expected to increase with rising water temperature. Yet, the distribution and prevalence of *T. bryosalmonae* in Northern Europe remain poorly characterized. Here, we studied 43 locations in 27 rivers in northernmost Norway and Finland to describe *T. bryosalmonae* infection frequency and patterns in 1389 juvenile salmonids. *T. bryosalmonae* was discovered in 12 out of 27 rivers (44%) and prevalence ranged from 4.2 to 55.5% in Atlantic salmon and from 5.8 to 75% in brown trout among infected rivers. In sympatric populations, brown trout was more frequently infected with *T. bryosalmonae* than was salmon. Age-specific parasite prevalence patterns revealed that in contrast to lower latitudes, the infection of juvenile fish predominantly occurs during the second summer or later. Temperature monitoring over 2 yr indicated that the mean water temperature in June was 2.1 to 3.2°C higher in rivers containing *T. bryosalmonae* compared to parasite-free rivers, confirming the important role of temperature in parasite occurrence. Temporal comparison in *T. bryosalmonae* prevalence over a 10 yr period in 11 rivers did not reveal any signs of contemporary parasite spread to previously uninfected rivers. However, the wide distribution of *T. bryosalmonae* in rivers flowing to the Barents Sea indicates that climate change and heat waves may cause new disease outbreaks in northern regions.

KEY WORDS: Fish disease · Myxozoa · Climate change · Proliferative kidney disease · *Tetracapsuloides bryosalmonae* · *Salmo salar* · *Salmo trutta* · *Salvelinus alpinus*

1. INTRODUCTION

Global warming has a profound impact on the geographical expansion, abundance and virulence of many pathogens (Kutz et al. 2009, Callaway et al. 2012, Gallana et al. 2013), and temperature-driven environmental stress may further increase the risk of disease (Marcogliese 2008, Niinemets et al. 2017). The impact of global warming has been particularly severe in polar regions (Post et al. 2019, Previdi et al.

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2021), where aquatic ecosystems experience extreme alterations in run-off regime, water chemistry, nutrients and temperature dynamics (IPCC 2021).

Tetracapsuloides bryosalmonae is an endoparasitic myxozoan causing proliferative kidney disease (PKD) in salmonid fishes (Canning et al. 1998). The parasite has a 2-host life cycle, alternating between bryozoans and salmonid fish in freshwater (Anderson et al. 1999). Juvenile fish are infected with the parasite predominantly during their first growth season (Mo et al. 2011, Okamura et al. 2011, Dash & Vasemägi 2014) through gills and skin by infective spores released from bryozoans (Longshaw et al. 2002). Development of clinical disease symptoms, including renal proliferation and anemia, is influenced by water temperature and it usually takes 4 to 8 wk post-infection for the clinical signs to be fully developed after water temperature has reached 15°C (Clifton-Hadley et al. 1986). The abundance of parasite stages infective to fish is linked to rising temperatures, which affects bryozoan biomass and abundance of infective parasite spores within the environment (Tops et al. 2006, 2009, Hartikainen et al. 2009). Bryozoan biomass is also positively influenced by increased nutrient concentrations in water, reflecting productivity gradients in rivers (Hartikainen et al. 2009). Thus, the severity of PKD is dependent on temperature through the emergence of the clinical course of the disease and elevated bryozoan biomass, which promotes higher parasite abundance. However, despite the widely contemplated connection between global warming and *T. bryosalmonae* spread (Tops et al. 2006, Okamura et al. 2011, Sudhagar et al. 2019, Borgwardt et al. 2020, Ros et al. 2022), we currently lack field evidence to demonstrate the actual expansion of the parasite distribution towards higher latitudes or the consistent increase in the prevalence of the infection over time.

T. bryosalmonae is widely distributed in temperate regions of Europe, ranging from Spain to Norway and from Iceland to Estonia (Peribáñez et al. 1997, Feist et al. 2002, Kristmundsson et al. 2010, Skovgaard & Buchmann 2012, Jenčič et al. 2014, Dash & Vasemägi 2014, Mo & Jørgensen 2017, Oredalen et al. 2022, Svavarsdóttir et al. 2021). Additionally, *T. bryosalmonae* has been found close to 65° N latitude in Alaska, and in northern Norway and Finland (Kristmundsson et al. 2010, Vasemägi et al. 2017, Mo & Jørgensen 2017, Sobociński et al. 2018, Gorgoglione et al. 2020, Svavarsdóttir et al. 2021). Known bryozoan hosts of *T. bryosalmonae*, such as *Fredericella sultana*, *F. indica* and *Cristatella mucedo* (Longshaw et al. 1999, Okamura & Wood 2002, Hartikainen et al. 2013), are also found in northern Norway (Økland & Økland 2005). Although there exist a few records of *T. bryosalmonae* at higher latitudes (Mo & Jørgensen 2017), we currently lack more fine-scale information about the distribution and prevalence of *T. bryosalmonae* inhabiting northernmost European rivers. Yet, such knowledge is important considering that global warming and future heat waves may cause new PKD outbreaks in northern regions, where salmonid fishes have important economic, social and cultural value for local communities (Otero et al. 2012, Sternecker et al. 2014).

In this study, we screened *T. bryosalmonae* in 3 salmonid fish species encompassing 43 locations in 27 rivers and tributaries in northernmost Europe. Using molecular genetic analysis of kidney tissues collected from juvenile Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic char *Salvelinus alpinus*, we aimed to (1) gather detailed distributional data on *T. bryosalmonae* in northernmost Europe; (2) characterize age- and species-specific parasite prevalence patterns; (3) evaluate the association between parasite occurrence and water temperature in a subset of studied rivers; and (4) test whether *T. bryosalmonae* has spread to previously uninfected rivers or increased its prevalence during the last 10 yr by comparing the current situation to earlier data from 2008 as described by Mo & Jørgensen (2017).

2. MATERIALS AND METHODS

2.1. Sampling of fish and measurement of water temperature

During late September 2019 and early November 2020, a total of 1368 salmonids were sampled from 27 rivers (43 locations) flowing into the Barents Sea and Norwegian Sea in northernmost Norway and Finland (Fig. 1). Juvenile fish were caught by electrofishing (permits 2019/11137, 2019/14374 and 2020/9204), following a random sampling procedure as described in Ozerov et al. (2017). Waders and electrofishing equipment were disinfected when moving between sampling sites using 1% Virkon S solution (contact time at least 30 min) as recommended by Norwegian Food Safety Authority (Mattilsynet). Fish were euthanized by concussion according to Directive 2010/63/EU of the European Parliament and of the Council on the Protection of Animals used for Scientific Purposes (https://eur-lex.europa.eu/eli/dir/2010/63/oj).

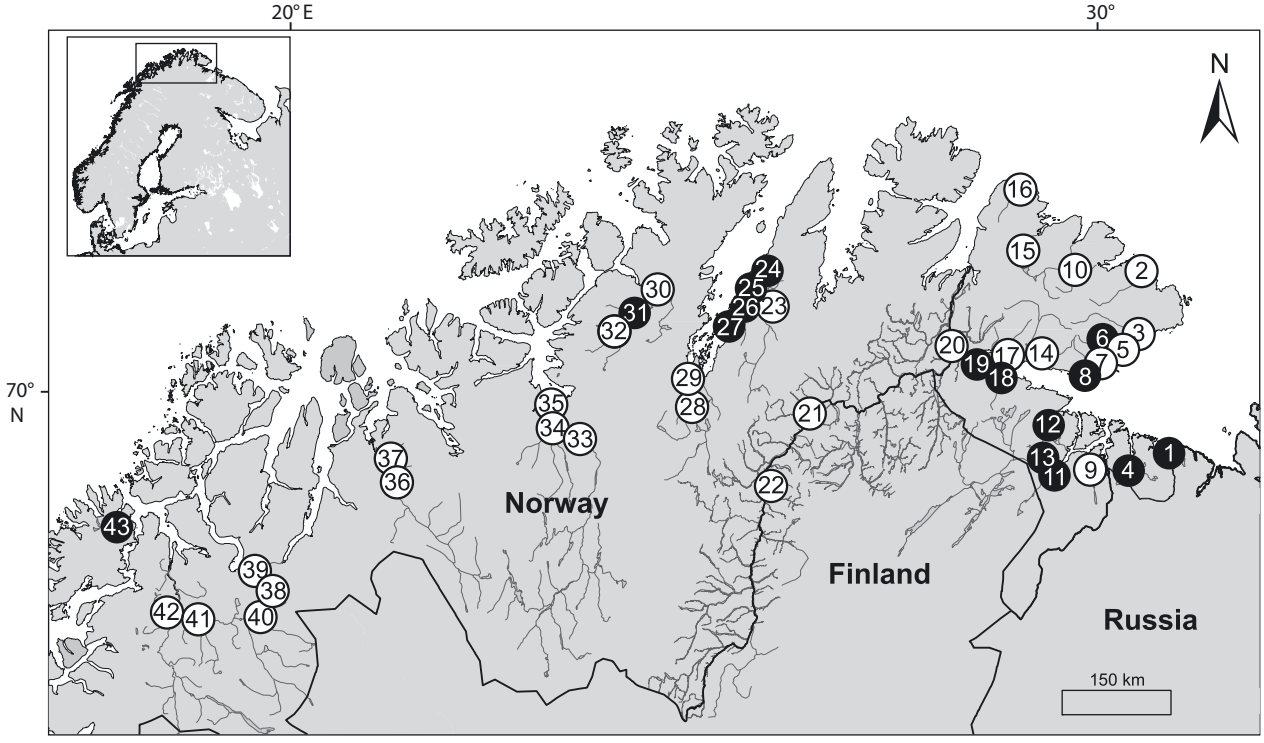

Fig. 1. Map of studied rivers and occurrence of *Tetracapsuloides bryosalmonae*. Numbers refer to the sampling locations (Tables 1 and 2). Circles indicate *T. bryosalmonae* presence (black) and absence (white) in studied locations

Collected fish were stored individually in plastic bags and immediately frozen for transport to the laboratory. In the laboratory, the fish were thawed for measurement of total length and weight similar to as described in Oredalen et al. (2022). Subsequently, using a sterile scalpel, a cross-section was produced by cutting the body between the front tip and the end of the dorsal fin as in Bruneaux et al. (2017). This body section was then stored in 96% ethanol for fixation and dissection of kidney tissue for subsequent molecular detection of *Tetracapsuloides bryosalmonae* (Dash & Vasemägi 2014). Hourly water temperature changes were measured using Tinytag® Aquatic 2 temperature loggers from June 2019 until October 2020. We were able to retrieve temperature data from 15 rivers (see Fig. 5, Table 4).

2.2. DNA extraction and molecular analysis

Molecular analysis was performed in the Fish Genetics Laboratory of the Chair of Aquaculture, Estonian University of Life Sciences, and in the Laboratory of Genetics of the University of Turku. Total genomic DNA of 830 specimens was extracted at the Estonian laboratory from kidney tissues using 1-step Chelex double-stranded DNA extraction protocol as in Casquet et al. (2012). In addition, DNA from 538 individuals was extracted at the University of Turku following Elphinstone et al. (2003). Presence of parasites was determined by multiplex PCR, using a *T. bryosalmonae*-specific protocol developed by Dash & Vasemägi (2014). To amplify 298 bp of the 18S rRNA gene of the parasite, the primers PKX3F (5′-CTA AGT ACA TAC TTC GGT AGA-3′) and PKX4R (5′-CCG TTA CAA CCT TGT TAG GAA-3′) (Kent et al. 1998) were used. Additionally, a shorter 166 bp fragment of the *T. bryosalmonae* 18S rRNA gene was amplified using the primers PKD-realF (5′-TGT CGA TTG GAC ACT GCA TG-3′) and PKD-realR (5′-ACG TCC GCA AAC TTA CAG CT-3′) (Grabner & El-Matbouli 2009). As a positive amplification control, salmonid-specific reverse (5′-GAT TCT CAT GTT AGC CGT CCA-3′) and forward (5′-GCC CAA AAT GTA CAG GCA AT-3′) primers were used in a multiplex reaction to amplify a 500 bp fragment (Vasemägi et al. 2010). PCR product was loaded onto 2% agarose gel, stained with ethidium bromide and visualized under a UV transilluminator (UVItec FireReader; UVItec Limited). In total, 82 samples were excluded from the data set due to lack of amplification of the control salmonid fragment. Thus, the final data set consisted of 981 Atlantic salmon, 255 brown trout and 50 Arctic char samples (Tables 1 & 2). To confirm

Table 1. Prevalence of *Tetracapsuloides bryosalmonae* in Atlantic salmon *Salmo salar*. Rivers in bold have temporal parasite prevalence data from 2008 available (Mo & Jørgensen 2017). L indicates rivers with available water temperature data. Coordinates mark the lowermost downstream sampling station when a river has more than one sampling location. n: Number of studied fish in each age group; prevalence (%) of *T. bryosalmonae* with 95% confidence interval in brackets

Site no.	River	Coordinates (°N, °E)	Date (dd.mm.yyyy)	*T. bryosalmonae* infection status			
				0+ fish		1+ and older fish	
				n	Prevalence (95% CI)	n	Prevalence (95% CI)
1	Grense Jakobselva L	69°43′47″, 30°53′25″	21.09.2019	17	0 (0–18.4)	16	31.2 (14.2–55.6)
2	Sandfjordelva L	70°30′15″, 30°32′37″	29.09.2019			7	0 (0–35.4)
3	Komagelva L	70°14′28″, 30°30′20″	26.09.2019	8	0 (0–32.4)	13	0 (0–22.8)
4	Karpelva L	69°39′51″, 30°23′10″	22.09.2019			19	10.5 (2.7–31.4)
5, 6	Skallelva L	70°10′49″, 30°17′00″	25.09.2019	7	0 (0–35.4)	35	2.9 (0.5–14.5)
7	Storelva Vadsø	70°07′11″, 30°02′25″	28.09.2019			20	0 (0–16.1)
8	Sjøbuselv	70°03′48″, 29°53′47″	29.09.2019			13	0 (0–22.8)
9	**Neidenelva/Näätämö L**	69°41′25″, 29°23′00″	21.09.2019	16	0 (0–19.3)	25	0 (0–13.3)
10	Syltefjordelva L	70°31′20″, 29°25′43″	27.09.2019			4	0 (0–49)
11	Munkelva	69°38′54″, 29°27′32″	22.09.2019	9	0 (0–29.9)	18	83.3 (60.7–94.1)
12	Klokkerelva	69°51′27″, 29°23′14″	23.09.2019			22	0 (0–14.9)
13	Sandneselva L	69°40′02″, 29°54′29″	22.09.2019	2	0 (0–65.8)	16	50 (28–72)
14	**Vestre Jakobselv**	70°07′03″, 29°18′51″	26.09.2019	2	0 (0–65.8)	15	0 (0–20.4)
15	**Kongsfjordelva L**	70°35′44″, 29°05′13″	27.09.2019	2	0 (0–65.8)	17	0 (0–18.4)
16	Storelva Berlevåg L	70°50′27″, 29°02′31″	28.09.2019	3	0 (0–56.2)	17	0 (0–18.4)
17	Bergebyelva L	70°09′04″, 28°54′02″	24.09.2019	5	0 (0–43.5)	20	0 (0–16.1)
18	Nyelva L	70°04′01″, 28°49′32″	23.09.2019			19	15.8 (5.5–37.6)
19	Vesterelv L	70°06′58″, 28°30′24″	24.09.2019	7	0 (0–35.4)	19	10.5 (2.9–31.4)
20–22	**Tana/Teno L**	70°11′42″, 28°11′41″	08.11.2020	58	0 (0–6.2)	59	0 (0–6.1)
23–27	**Børselva**	70°19′00″, 25°34′31″	12.11.2020	8	0 (0–32.4)	106	7.5 (3.9–14.2)
28, 29	Lakselva Porsanger	69°55′59″, 24°58′35″	10.11.2020	12	0 (0–24.3)	52	0 (0–6.9)
30–32	**Repparfjordelva**	70°20′02″, 24°16′38″	9.11.2020	9	0 (0–29.9)	55	9.1 (4–19.6)
34, 35	**Altaelva**	69°52′03″, 23°18′35″	11.11.2020	5	0 (0–43.5)	53	0 (0–6.8)
36, 37	**Reisaelva**	69°40′33″, 21°15′53″	10.11.2020	24	0 (0–13.8)	48	0 (0–7.4)
39	**Nordkjoselva**	69°12′35″, 19°36′49″	11.11.2020	1	0 (0–79.4)	1	0 (0–79.4)
40, 41	**Målselva**	69°01′34″, 19°27′37″	9.11.2020	22	0 (0–14.9)	31	0 (0–11)
43	**Lyselva**	69°24′54″, 17°51′44″	11.11.2020	34	0 (0–10.2)	10	30 (10.8–60.3)

Table 2. Prevalence of *T. bryosalmonae* in brown trout *Salmo trutta*. L indicates rivers with available water temperature data. Coordinates mark the lowermost downstream sampling station when a river has more than one sampling location. n: Number of studied fish in each age group; prevalence (%) of *T. bryosalmonae* with 95% confidence interval in brackets

Site no.	River	Coordinates (°N, °E)	Date (dd.mm.yyyy)	*T. bryosalmonae* infection status			
				0+ fish		1+ and older fish	
				n	Prevalence (95% CI)	n	Prevalence (95% CI)
1	Grense Jakobselva L	69°43′47″, 30°53′25″	21.09.2019			5	40 (11.7–76.9)
3	Komagelva L	70°14′28″, 30°30′20″	26.09.2019			2	0 (0–65.7)
6	Skallelva L	70°11′01″, 30°11′19″	25.09.2019			14	42.9 (21.3–67.4
8	Sjøbuselv	70°03′48″, 29°53′47″	29.09.2019			21	19 (7.6–40)
14	Vestre Jakobselv	70°07′03″, 29°18′51″	26.09.2019			1	0 (0–79.3)
18	Nyelva L	70°04′01″, 28°49′32″	23.09.2019	1	0 (0–79.3)	19	26.3 (11.8–48.8)
19	Vesterelv L	70°06′58″, 28°30′24″	24.09.2019			16	18.8 (4–45.6)
24–27	Børselva	70°19′00″, 25°34′31″	12.11.2020	1	0 (0–79.3)	16	62.5 (53.5–87.4)
29	Lakselva Porsanger	70°03′21″, 24°54′58″	10.11.2020	4	0 (0–49)	3	0 (0–56.2)
33, 35	Altaelva	69°49′59″, 23°28′50″	11.11.2020	1	0 (0–79.3)	14	0 (0–21.5)
36, 37	Reisaelva	69°40′33″, 21°15′53″	10.11.2020	11	0 (0–25.9	23	0 (0–14.3)
38, 39	Nordkjoselva	69°12′35″, 19°36′49″	11.11.2020	28	0 (0–12.1)	48	0 (0–7.4)
41, 42	Målselva	69°01′34″, 19°27′37″	9.11.2020	6	0 (0–39)	1	0 (0–79.3)
43	Lyselva	69°24′54″, 17°51′44″	11.11.2020	12	8.3 (1.5–35.4)	8	25 (7.2–59.1)

the presence of *T. bryosalmonae*, we also used Sanger sequencing from both the forward and reverse direction using PKX3F and PKX4R primers.

2.3. Statistical analysis

Based on our measured length and weight data and published age and size information (Jensen et al. 1998), salmon and trout smaller than 1 g were classified as young-of-the-year (0+). Wilson's score method was used to calculate 95% confidence intervals for parasite prevalence using a web-based calculator (http://vassarstats.net/prop1.html). Differences in *T. bryosalmonae* prevalence between age groups (0+ versus older), species (Atlantic salmon versus brown trout) and current (2019–2020) and historical data (samples collected in 2008; Mo & Jørgensen 2017) were tested using a non-parametric Wilcoxon test for paired samples. When differences in *T. bryosalmonae* prevalence between Atlantic salmon and brown trout were tested, 0+ fish were excluded from the analysis, since we observed that the infection occurs predominantly during later life stages (see below). Similarly, 0+ fish were excluded from the comparison of current and historical data (Mo & Jørgensen 2017), because the prevalence estimates of the latter work were based on 1+ and older Atlantic salmon specimens. We further evaluated the inconsistencies between data from Mo & Jørgensen (2017) and our data set for 3 rivers (Tana/Teno, Neidenelva/Näätämö, Kongsfjordelva), where we did not observe *T. bryosalmonae*. More specifically, we used Microsoft Excel add-in PopTools 3.2 (Hood 2010) to evaluate whether the lack of parasites in our data set could have been caused by limited sample size, assuming that the true prevalence of *T. bryosalmonae* in these rivers was as reported in Mo & Jørgensen (2017). To do this, we used a Monte Carlo analysis procedure with resampling and replacement option, consisting of 10 000 simulations. Differences in average monthly water temperatures from May to August, number of days >10°C and 15°C, and degree-days (June to August) between infected and parasite-free rivers were tested using a *t*-test. We applied a one-sided test, since we expect that abundance and occurrence of *T. bryosalmonae* are positively affected by water temperature. A correlation test was used to test the interaction of temporal water temperature parameters and parasite prevalence between infected and uninfected rivers. All statistical tests were carried out using the statistical software R 4.1.0 (R Foundation for Statistical Computing) and MS Excel (Microsoft Corporation 2018). Figures were constructed using the plotting package ggplot2 (v. 3.3.5; Wickham 2016) in R 4.1.0.

3. RESULTS

3.1. Distribution of *Tetracapsuloides bryosalmonae* in northernmost Europe

Atlantic salmon and brown trout from 12 of 27 rivers (44%) were infected with *T. bryosalmonae*. The infected rivers were widely distributed, ranging from Grense Jakobselva in eastern Finnmark to Lyselva at Senja Island (Fig. 1). At the same time, the distribution of the parasite was rather heterogeneous. For example, *T. bryosalmonae* was found in 9 of 14 rivers flowing to Varangerfjord; meanwhile, the myxozoan parasite was absent in the majority of other studied rivers in Troms and Finnmark counties. Overall, the prevalence of *T. bryosalmonae* was rather low in both Atlantic salmon (5.3%, 52 infected individuals out of 981) and brown trout (12.9%, 33 infected individuals out of 255; Tables 1 & 2). For 2 infected rivers, more than one sampling location was studied. In the river Børselva, samples were collected from 5 locations: 2 sites in mainstream lower reaches (location nos. 26 and 27) and in 2 tributaries (2 locations in Børselva-Ailigas and one in Børselva-Vieksa). Prevalence of *T. bryosalmonae* was highest in Ailigas (33.3%, n = 45, location nos. 24 and 25 both contained infected salmonids), which flows into mainstream Børselva at the lower reaches, about 10 km from the river mouth. In contrast, downstream prevalence of mainstream Børselva was 4.9% (n = 61), whereas no infected salmonids were found in the upper tributary Vieksa (location no. 23, n = 25). The river Repparfjordelva consisted of 3 sampling locations in lower to mid reaches of the river and infected salmonids were found only at the middle sampling location with a prevalence of 41.6% (n = 12, location no. 31). None of the studied char samples, collected from 5 rivers showed evidence of *T. bryosalmonae* infection (Table 3). Similarly, we did not find infected Atlantic salmon nor brown trout in these 5 rivers. Sanger sequencing of the infected Atlantic salmon individual from the River Sandneselva (GenBank accession ON740974) confirmed the presence of *T. bryosalmonae* showing very high similarity (99.6%) with multiple available *T. bryosalmonae* sequences (e.g. KJ150279, KJ150280, KJ150284, KJ150285, KJ150286, MG775220, MG775221, MG775222, MT002360.1, MT002366, KF805631).

Table 3. Prevalence of *T. bryosalmonae* in Arctic char *Salvelinus alpinus*. L indicates rivers with available water temperature data. n: Number of studied fish in each age group; prevalence (%) of *T. bryosalmonae* with 95% confidence interval in brackets

Site no.	River	Coordinates (°N, °E)	Date (dd.mm.yyyy)	*T. bryosalmonae* infection status			
				0+ fish		1+ and older fish	
				n	Prevalence (95% CI)	n	Prevalence (95% CI)
2	Sandfjordelva L	70°30′15″, 30°32′37″	29.09.2019			20	0 (0–16.1)
10	Syltefjordelva L	70°31′20″, 29°25′43″	27.09.2019	1	0 (0–79.3)	13	0 (0–22.8)
16	Storelva Berlevåg L	70°50′27″, 29°02′31″	28.09.2019			14	0 (0–21.5)
37	Reisaelva	69°40′33″, 21°15′53″	10.11.2020			1	0 (0–79.3)
41	Målselva	69°01′34″, 19°27′37″	9.11.2020			1	0 (0–79.3)

3.2. Age- and inter-specific differences in *T. bryosalmonae* prevalence

Analysis of age-specific parasite prevalence patterns revealed that all analyzed 0+ Atlantic salmon were free of *T. bryosalmonae*, which suggests that the infection of juvenile salmon takes place at later life stages (Wilcoxon test, p = 0.014; Fig. 2a). A similar trend for higher prevalence of older year-classes was evident in brown trout, albeit the Wilcoxon test did not reach a formal level of significance, most likely because of the low number of locations (Wilcoxon test, p = 0.059; Fig. 2b). In 10 studied rivers where brown trout and Atlantic salmon occurred in sympatry, brown trout were more frequently infected with *T. bryosalmonae* than salmon (Wilcoxon test, p = 0.022; Fig. 3).

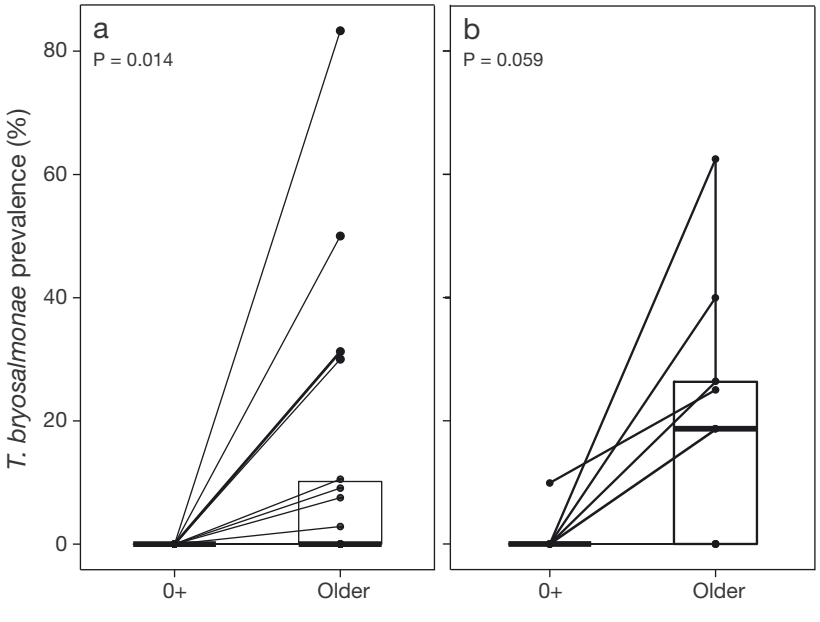

Fig. 2. Difference in prevalence of *T. bryosalmonae* between 0+ and older year-classes in (a) Atlantic salmon and (b) brown trout. Dots connected with a line represent 2 year-classes in the same river; boxes represent the interquartile range with the median as a bold line and whiskers showing 95% quantiles

3.3. Temporal differences in *T. bryosalmonae* prevalence

In order to test whether *T. bryosalmonae* has spread to formerly parasite-free rivers, we compared our findings with the 2008 data collected by Mo & Jørgensen (2017). Based on analysis of 11 overlapping rivers, we found no evidence of *T. bryosalmonae* spreading to formerly parasite-free rivers (Fig. 4). Furthermore, in contrast to our expectations, we did not detect any increase in *T. bryosalmonae* prevalence over time. In fact, more recent estimates were lower than most *T. bryosalmonae* prevalence estimates from 2008, although a non-parametric Wilcoxon test did not formally support the temporal change in median prevalence values at the 5% significance level (Wilcoxon test, p = 0.059; Fig. 2b). In 3 rivers, we did not find *T. bryosalmonae*, as opposed to Mo & Jørgensen (2017), who reported low to moderate parasite prevalence in the same rivers (Neidenelva 6.7%, Tana/Teno 10.1%, Kongsfjordselva 33.3%). Therefore, we used a Monte Carlo resampling approach to test whether this inconsistency could be explained by the limited number of studied samples, combined with low parasite prevalence. For Neidenelva, using 25 individuals was not sufficient to encounter parasites in 17.7% of simulations (1765 cases out of 10 000), when the true parasite prevalence was only 6.7% as reported in Mo & Jørgensen (2017). In contrast, our sample sizes should have been sufficient to detect parasite in Tana/Teno and Kongsfjordselva, as we did not encounter the parasite only in 0.19% and 0.08% of simulations, when the

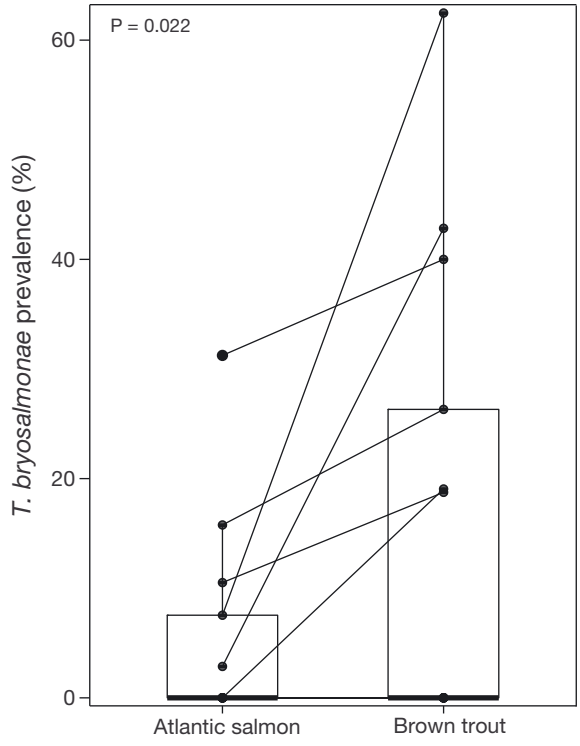

Fig. 3. Difference in prevalence of *T. bryosalmonae* in sympatric Atlantic salmon and brown trout sampled from the same locations. Dots connected with a line represent 2 groups in the same location; boxes represent the interquartile range with the median as a bold line and whiskers showing 95% quantiles

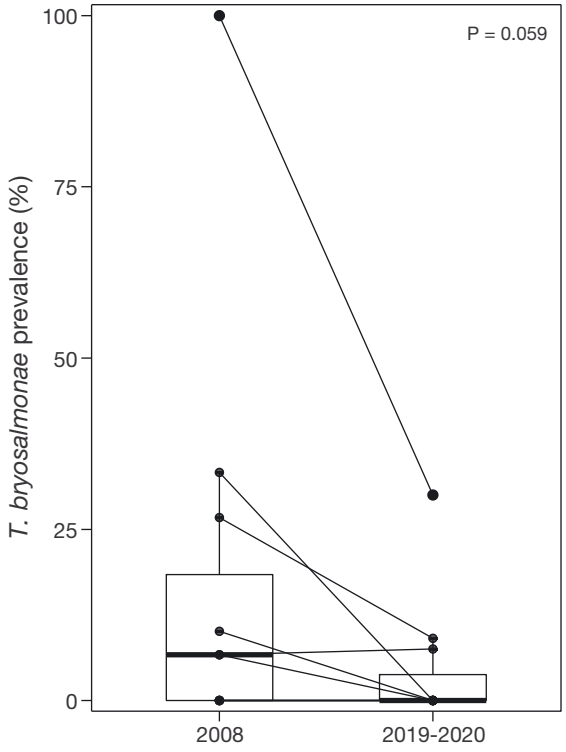

Fig. 4. Temporal change in prevalence of *T. bryosalmonae* in Atlantic salmon over a 10-yr period. Data from 2008 are derived from Mo & Jørgensen (2017). Dots connected with a line represent 2 groups of the same river; boxes represent the interquartile range with the median as a bold line and whiskers showing 95% quantiles

true parasite prevalence was 10.1% and 33.3%, respectively, as reported in Mo & Jørgensen (2017).

3.4. Association between water temperature and *T. bryosalmonae* occurrence

Only for 2 of 15 studied rivers did mean water temperature reach 15°C in July. Furthermore, the time period when water temperature exceeded 15°C was very brief even for the warmest rivers (Fig. 5). Analyses of average monthly water temperatures indicated that rivers harboring salmonids infected with *T. bryosalmonae* are generally warmer than parasite-free rivers (Table 4, Fig. 5). During both years, the average water temperature in June was significantly higher (2.13°C in 2019 and 3.22°C in 2020) in rivers where *T. bryosalmonae* was detected compared to parasite-free rivers. In 2020, the average water temperature was significantly higher in *T. bryosalmonae*-containing rivers also during May and July (0.62°C and 2.43°C, respectively). Furthermore, the average water temperature during the whole summer (June–August) and number of days >10°C in 2020 were higher in *T. bryosalmonae*-infected rivers ($p = 0.037$ and $p = 0.04$, respectively). However, evaluation of individual temperature profiles also revealed that some relatively warm-water rivers were parasite free (e.g. Neidenelva), whereas other, rather

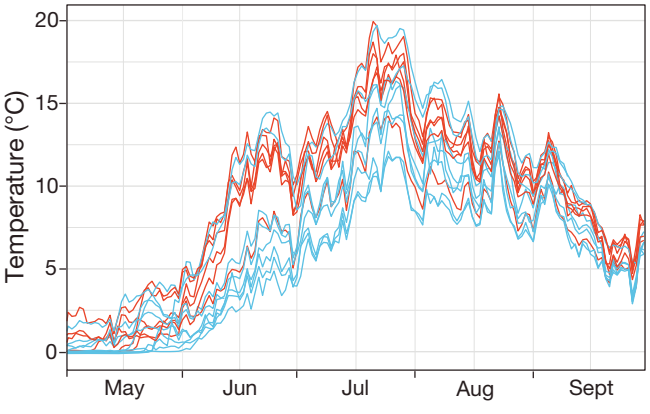

Fig. 5. Water temperature profiles of 15 rivers measured from June to October 2020. Red and light blue lines indicate rivers where *T. bryosalmonae* was present and absent, respectively

Table 4. Estimated monthly water temperature, number of days >10°C and >15°C, and degree-days (June to August) in 15 studied rivers in relation to *T. bryosalmonae* occurrence during 2019 and 2020. The difference in average monthly water temperatures between infected and parasite-free rivers is shown as Δ°C. Outcome from the 1-tailed *t*-test between infected and parasite-free rivers is presented as a p-value, and statistically significant p-values are shown in **bold**

Temperature measurement	2019				2020			
	T. bryosalmonae		Δ°C	p	*T. bryosalmonae*		Δ°C	p
	Absent	Present			Absent	Present		
May mean (°C)					0.66	1.29	0.62	0.058
June mean (°C)	7.68	9.81	2.13	**0.024**	6.80	10.02	3.22	**0.021**
July mean (°C)	10.78	12.01	1.23	0.112	11.33	13.76	2.43	**0.024**
August mean (°C)	9.64	10.64	1.00	0.103	10.95	12.05	1.10	0.126
June–August mean (°C)	9.58	10.86	1.28	0.071	9.23	11.32	2.09	**0.037**
Days >10°C	42	59	17	0.090	46	69	23	**0.040**
Days >15°C	5	6	1	0.293	7	12	5	0.133
Degree days June–August	779	889	110	0.071	820	991	171	**0.037**

cold-water rivers (e.g. Skallelva) tested positive (Fig. 5), suggesting that water temperature may not be the only factor influencing the spread and occurrence of *T. bryosalmonae* in the studied rivers. Estimated correlation coefficients between parasite prevalence and temporal water temperature parameters (monthly average temperatures, degree-days) were small and statistically non-significant (data not shown).

4. DISCUSSION

This study indicates that *Tetracapsuloides bryosalmonae* is common and widely distributed in northernmost European rivers reaching up to 400 km north of the Arctic Circle. In the following, we place these results into the context of global climate change and assess the implications of our findings in connection to the predicted future disease outbreaks in northern Europe.

Most of the studies on *T. bryosalmonae* to date have been conducted in temperate regions (Hedrick et al. 1993, Okamura et al. 2011), where clinical symptoms of PKD are often present (Ferguson 1981, Brown et al. 1991, Wahli et al. 2002, Bettge et al. 2009a,b, Borgwardt et al. 2020). This is because parasitological investigations are commonly invoked after disease outbreak or sudden fish death among farmed or, occasionally, wild fish (Seagrave et al. 1981, Sterud et al. 2007, Bettge et al. 2009b, Bailey et al. 2017, Bruneaux et al. 2017, Hutchins et al. 2021). However, much less is known about the distribution of the parasite and the effects of the disease at high latitudes in both Europe and North America. In Alaska, *T. bryosalmonae* has been recently detected close to the Arctic Circle, with clinical PKD symptoms (renal hyperplasia) observed in adult wild chum salmon and farmed sockeye salmon (Gorgoglione et al. 2020). In Iceland, clinical PKD has been reported in Arctic char and brown trout (Kristmundsson et al. 2010, Svavarsdóttir et al. 2021), while Atlantic salmon have shown subclinical phases of infection (Svavarsdóttir et al. 2021). In northeost Norway, *T. bryosalmonae* has been detected in 1+ and older Atlantic salmon parr (Mo & Jørgensen 2017). Our findings confirm the presence of *T. bryosalmonae* in juvenile Atlantic salmon at high latitudes and also indicate that the parasite regularly infects brown trout. In fact, when both species were sampled at the same location, brown trout was more frequently infected with *T. bryosalmonae* than was Atlantic salmon. This agrees with the recent findings from Lauringson et al. (2021), who showed that Atlantic salmon is more resistant against *T. bryosalmonae* compared to brown trout, being able to slow down initial parasite multiplication and subsequently tolerate high parasite burden without developing severe disease symptoms. In contrast to Atlantic salmon and brown trout, we did not find any *T. bryosalmonae* infections among studied Arctic char. This is likely due to the low number of collected specimens and limited sampling locations, since *T. bryosalmonae* is able to infect Arctic char (Kristmundsson et al. 2010, Mo & Jørgensen 2017, Svavarsdóttir et al. 2021, Oredalen et al. 2022).

In terms of parasite occurrence, we found *T. bryosalmonae* in 12 of 27 studied rivers (44%), whereas Mo & Jørgensen (2017) detected the parasite in 68% of rivers (15 of 22) in Nordland, Finnmark and Troms counties. Similarly, the overall prevalence of *T. bryosalmonae* in Atlantic salmon was much lower in our

data set (5.3%) compared to the corresponding estimate (29.4%) by Mo & Jørgensen (2017) from Nordland, Finnmark and Troms counties. Despite these differences, both our study and others indicate that *T. bryosalmonae* is commonly found in rivers north of the Arctic Circle and that the parasite prevalence is spatially highly variable.

One of the most striking findings of this study was the near absence of *T. bryosalmonae* infections among young-of-the-year juvenile fish. This was unexpected because to date, *T. bryosalmonae* has been found to predominantly infect salmonids during the first growing season (Okamura et al. 2011, Dash & Vasemägi 2014). Earlier work in the UK has shown that the concentration of infective *T. bryosalmonae* spores may peak in May to June (Fontes et al. 2017). Studies in Estonia have demonstrated how subsequent parasite proliferation in young-of-the-year fish takes place from June to September and parasite prevalence increases during the first growing season (Dash & Vasemägi 2014, Lauringson et al. 2021). However, the environment at high latitudes is much harsher, and near 70°N, the growing season for juvenile salmonids is limited to only 3 mo (Jensen 2003). For Atlantic salmon and brown trout, the first growing season is further shortened because the emergence from the gravel and exogenous feeding starts as late as the end of June or July (Jensen et al. 1991, E. Niemelä unpubl. data). As a result, the mass of 0+ Atlantic salmon in northernmost European rivers is typically less than 1 g by the end of August. Late emergence may therefore play an important role in the infection dynamics, as young-of-the-year fish are likely first exposed to parasite spores in July or even later. Furthermore, despite the fact that bryozoans tolerate a broad range of environmental conditions (Wood 2010), the oligotrophic and cold environment generally suppresses their reproduction and biomass (Hartikainen et al. 2009, Wood 2010). Therefore, late emergence from the gravel combined with low bryozoan biomass and parasite spore density are likely the main factors causing near absence of *T. bryosalmonae* infections among young-of-the-year fish.

Water temperature is the main driver in infection dynamics, PKD progression and mortality since higher water temperature enhances bryozoan biomass, increases spore production and promotes disease development (Bettge et al. 2009a,b, Hartikainen et al. 2009, Tops et al. 2009, Bruneaux et al. 2017, Strepparava et al. 2018, Ahmad et al. 2021). Furthermore, an increase of water temperature by 1°C has been estimated to raise prevalence of *T. bryosalmonae* among infected wild brown trout by 5.7% (Rubin et al. 2019). Yet, only a handful of field studies to date have evaluated the relationships between parasite occurrence and seasonal water temperature (Hari et al. 2006, Lewisch et al. 2018, Rubin et al. 2019, Borgwardt et al. 2020). Based on analyses of 15 rivers over 2 yr (18 locations), we discovered that *T. bryosalmonae* can be found in much colder waters than previously reported. For example, based on 45 stations located over 18 rivers in Switzerland, Rubin et al. (2019) found that all studied sites were free from *T. bryosalmonae* when the mean water temperature was below 14°C in June. In contrast, based on our temperature measurements, the mean water temperature in June ranged from 6.3 to 12.0°C in rivers where *T. bryosalmonae* was recorded. Furthermore, even during July water temperatures exceeded 14°C only for a short period of time for few studied rivers. Yet, despite the drastic differences in water temperature between our study and other studies from warmer regions, we found that the average monthly water temperature was higher (2.1–3.2°C in June, 1.2–2.4°C in July) in rivers where *T. bryosalmonae* was present, as opposed to parasite-free rivers. This corroborates other field studies in temperate regions (El-Matbouli & Hoffmann 2002, Rubin et al. 2019, Waldner et al. 2020). Thus, it is likely that an increase of water temperatures by 2–3°C will also trigger earlier, more intense and longer *T. bryosalmonae* exposure for salmonid hosts in the northernmost European rivers.

Because of strong temperature dependence, several studies have predicted that climate change will provoke more frequent and severe outbreaks of PKD, and promote further spread of *T. bryosalmonae* (e.g Tops et al. 2009, Okamura et al. 2011). Yet, despite expectations, we lack temporal evidence to document the spread of the parasite towards northern regions or to previously parasite-free rivers. Here, we took advantage of published data collected in 2008 (Mo & Jørgensen 2017) and compared it with *T. bryosalmonae* presence and prevalence in 2019–2020. To our surprise, we did not find evidence for temporal increase in parasite prevalence nor did we observe the spread of *T. bryosalmonae* to previously uninfected rivers. Furthermore, we did not find the parasite in 3 rivers in which it was previously detected (Tana/Teno, Neidenelva/Näätämö and Kongsfjordelva). This can be explained by several, non-mutual factors. Firstly, our simulations showed that at least for one river (Kongsfjordelva), the inconsistency between the 2 data sets can be attributed to the small number of samples if the true parasite prevalence is

low. Secondly, annual variation in summer temperature can potentially influence *T. bryosalmonae* prevalence among salmonid hosts (Dash & Vasemägi 2014, Carraro et al. 2016, A. Vasemägi unpubl. data). Yet, mean air temperature in northernmost Norway in summer 2008 (9.98°C) was slightly colder than in 2019 and 2020 (10.07 and 12.01°C, respectively; Norwegian Centre for Climate Services, https://seklima.met.no/). Thirdly, differences related to sampling locations along the river may generate variation in parasite prevalence estimates, since the frequency of *T. bryosalmonae* can vary even over small spatial scales as a result of local hydrological conditions (Carraro et al. 2016, Debes et al. 2017). However, differences between sampling locations are unlikely to generate systematic bias in parasite prevalence estimates across multiple watersheds. Finally, differences in parasite detection sensitivity between molecular assays may potentially create bias in parasite prevalence estimates. In our work, we employed a multiplex PCR approach (30 amplification cycles) followed by agarose gel electrophoresis and manual recording of parasite fragments similar to Dash & Vasemägi (2014), whereas Mo & Jørgensen (2017) used real-time PCR with SYBR Green chemistry (38 cycles). Both of these methods have specific strengths and weaknesses. For example, identifying unspecific amplicons is straightforward with multiplex PCR, whereas parasite fragments that are very weakly amplified may be harder to score consistently. In contrast, although qPCR may increase the assay sensitivity, it is not trivial to separate non-specific amplification products from the true targets using SYBR Green chemistry. Thus, without direct comparison of the sensitivity and accuracy of different assays, it is difficult to assess their effect on current parasite prevalence estimates.

During the last 50 yr, the annual mean surface temperature in the Arctic has already increased by 3.1°C, which is 2 times higher than the global rate (IPCC 2021). Furthermore, warming of the Arctic continues and the mean annual surface air temperature is expected to rise by 3.3°C to 10°C by the year 2100 depending on future emission rates (AMAP 2021). Therefore, an abrupt rise in water temperature is also expected, which can trigger earlier, more intense and longer *T. bryosalmonae* exposure of salmonid hosts, favor the expansion of *T. bryosalmonae* and increase the probability of severe clinical PKD (Ros et al. 2022). Climatic conditions are also becoming seasonally more inconsistent (IPCC 2021), and extended heat waves can further expand short-term (cumulative) negative effects, increasing the possibility of severe PKD outbreaks (Sterud et al. 2007, Hutchins et al. 2021). However, the impact of PKD will likely vary among salmonid species, driven by inter-specific differences in PKD susceptibility (Grabner & El-Matbouli 2009, Syrová et al. 2020, Lauringson et al. 2021). Therefore, we expect that climate-change-driven PKD mortality will have a more severe impact on brown trout compared to Atlantic salmon populations in the future (Lauringson et al. 2021). Besides global climatic processes, local anthropogenic effects functioning at the watershed level may increase PKD-related mortality (Sterud et al. 2007). These include activities such as building of human-made reservoirs (Sterud et al. 2007), inflow of excess nutrients (Hartikainen et al. 2009), deforestation and removal of riparian shading (Ros et al. 2022), which reduce water flow, and increase water temperature and biomass production. However, it also provides an opportunity to develop measures that mitigate the adverse effects of temperature-dependent PKD on salmonid populations (Ros et al. 2022).

5. CONCLUSIONS

This study provided new knowledge on the distribution, prevalence and thermal preferences of *T. bryosalmonae* in northernmost Europe. Given that climate change and future heat waves are expected to cause new PKD outbreaks in northern regions, our work contributes towards a better understanding of the parasite epidemiology and contributed to the conservation of current salmonid populations. Our analyses also provide new information about age-dependent infection patterns in juvenile salmonids and confirm the higher resistance of Atlantic salmon in relation to sympatric brown trout.

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