Journal of Biogeography

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Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

The Pathobiome of *Salmo trutta* From the North Sea to the Barents Sea

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Received: 8 April 2024 | **Revised:** 18 October 2024 | **Accepted:** 31 October 2024

Funding: This work was supported by Norges Forskningsråd.

Keywords: aquaculture | biogeography | Ichthyobodo spp.; *Branchiomonas cysticola*; *Parvicapsula pseudobranchicola* | non-metric multidimensional scaling | pathogen | salmonids

ABSTRACT

Aim: Salmonids are some of the best studied species with respect to their pathobiome, and at the northern range limit, there is potential for pathogens to expand with both climate change and increased fish farming in the north.

Location: We sampled sea-run brown trout from throughout Norway for gill tissue and conducted both pooled and individual screenings for a total of 47 pathogens.

Time Period: Samples were collected during spring in 2020 and 2021.

Major Taxa: Bacteria, viruses and parasites of sea-run brown trout.

Methods: Brown trout were gill biopsied as part of the national sea lice monitoring programme and samples were sent for laboratory analysis using the Fluidigm system, which screened for a broad panel of different pathogenic species.

Results: Permutated multivariate analysis of variance revealed that the pathobiome richness of trout was more related to latitude than to fish farming biomass in the region where samples were taken. However, non-metric multidimensional scaling revealed a significant association between the individual pathobiome and the number of copepodid-stage *Lepeophtheirus salmonis* lice, which did reveal a south/central versus northern Norway segregation in pathogen distributions. Importantly, many pathogens positively associated with sea lice in southern/central Norway are known to be carried, and potentially transmitted by sea lice.

Main conclusions: In northern Norway, pathogens normally associated with infection and disease in trout were more commonly observed. However, given that most pathogens were detected from southern to northern Norway, it appears that further expansion of farms in the north are not likely to lead to further introductions of pathogens into northern areas of Norway, although it could amplify the prevalence of these pathogens on wild salmon.

1 | Introduction

The pathobiome consists of a diverse suite of microparasite and pathogenic species that are hosted by an organism; many of these species have the potential to cause disease (Bass et al. 2019). For species with broad geographic distributions, the pathobiome can affect life history, behaviour and immune function (Marcogliese 2004; Dionne et al. 2009; Vollset et al. 2014; Chretien et al. 2023). This variation can be attributed to various factors including biogeography, such that individuals may experience different pathogen loads at the range centre than the edge (Phillips et al. 2010; Bozick and Real 2015). Migratory species that cross boundaries may transport pathogens to novel areas and expand the distribution of those species or limit the spread of the pathogen by altering their environmental experience and challenging the physiological tolerance (Altizer et al. 2006).

In the northern hemisphere, salmonids form strong linkages between freshwater and marine environments via a seasonal cycle of movements in and out of river systems (Childress and McIntyre 2015). Native to systems from Portugal all the way to the Barents Sea, sea-run brown trout (*Salmo trutta*) is one of the most phenotypically diverse fish species (Birnie-Gauvin, Thorstad, and Aarestrup 2019; Ferguson et al. 2019). Sea-run brown trout also hold significant cultural, ecological and economic value (Lobón-Cerviá and Sanz 2017; Liu, Bailey, and Davidsen 2019). This value has recently been threatened by the presence and spread of marine aquaculture, and the resulting disease outbreaks (Vollset et al. 2014, 2018, 2023). Norway is one of the largest producers of farmed Atlantic salmon (*Salmo salar*) in the world, exporting more than 1.2 million metric tons of farmed salmonids (including Atlantic salmon and rainbow trout *Oncorhynchus mykiss*) per year (Norwegian Directorate of Fisheries 2022). Fish farming production is divided into 13 production zones, with the highest density of farms in the southwestern regions where the density exceeds 20 metric tons per km^2 in some of the highest density areas (production area 2–4, Vollset et al. 2017). The biogeographic gradient in farm production is liable to generate stronger pathogen spillback to wild fish in the southern parts of Norway; however, this gradient will soon shift, because the new regulatory approach, the Traffic Light System (Vollset et al. 2017; Myksvoll et al. 2018), is curtailing farm production in these southern areas and allowing increasing biomass of farms in the northern areas. This has the potential to generate aquaculture environmental interactions particularly if the pathobiome of wild fish is different in northern compared to southern populations.

With a changing climate and human influences on pathogen distribution related to fish farming, the lack of knowledge about salmonid pathogen biogeography in Norway is a factor that limits effective management. Specifically for sea-run brown trout, a species that is very exposed and vulnerable to pathogen spillover from fish farms and that has a broad distribution across climatic zones (Finstad et al. 2021), knowledge of the pathobiome and how it relates to latitude and aquaculture intensity remains limited. Using replicated sampling and molecular screening for bacteria, viruses and parasites from gill tissue, we evaluated two competing hypotheses. The first hypothesis was that sea-run brown trout pathogen biodiversity was related to a biogeographic gradient because northern latitudes are characterised by fewer and less diverse pathogens (Hoberg et al. 2012) and there are fewer cold-adapted pathogens that thrive in northern environments (Scheiner 2009). The alternative hypothesis was that there would be no biogeographic gradient in pathogen richness or diversity but that these would be related to local farmed salmon production. Using a broad panel for identifying pathogen presence in trout gill samples, we applied high throughput qPCR to characterise the pathobiome of sea-run brown trout across 13° of latitude. This study represents the first time that such genetic technology has been applied to screen a range of salmonid populations distributed along a latitudinal gradient in the Northeast Atlantic. The samples were collected during annual sea lice monitoring on sea-run brown trout along the Norwegian coast and allowed us to assess the coinfections with this prevalent ectoparasite that has been associated with fish farming intensity.

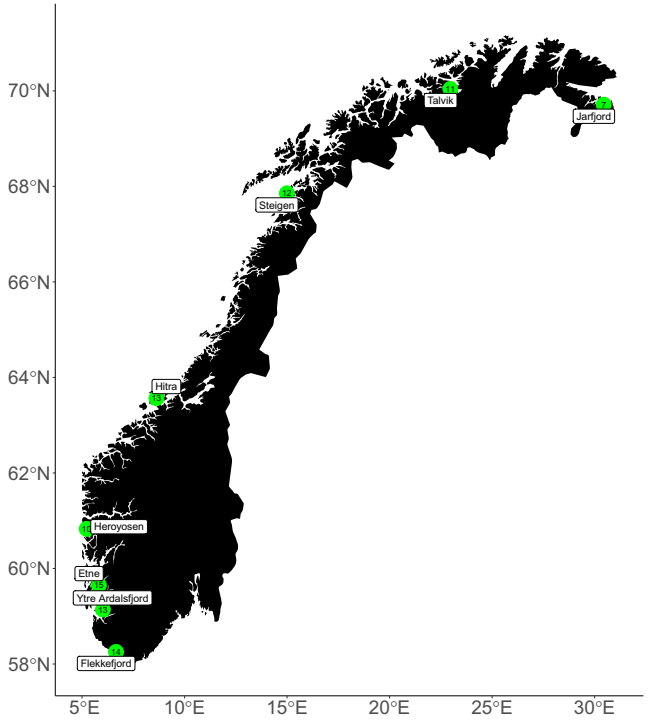

FIGURE 1 | Map of Norway and sampling sites in the Norwegian sea lice monitoring program. Samples were pooled from trout at all locations. Individual trout data were run from Jarfjord, Talvik, Steigen, Etne, Ytre Årdalsfjord, Herøyosen, Hitra and Flekkefjord. The total number of unique pathogen species detected at each site is written inside green points.

2 | Methods

2.1 | Fish Sampling

Sea-run brown trout were collected at sea during June and July in the years of 2020–2022 in the Norwegian National Lice Monitoring Program (NALO, Karlsen et al. 2022; Figure 1) using fyke nets and gillnets according to the standard protocols for the area. Sampled fish were killed at capture according to the NALO standard operating procedure, and gill samples were taken using sterilised equipment and stored in RNALater and subsequently frozen. After killing, the fish followed standard NALO protocols where the mass and length of the fish were

noted and sea lice were counted. Fish sampling was permitted by the Norwegian Environmental Directorate as part of the NALO program (document 2020/2710).

2.2 | Sea Lice Counting

Sea lice counting was completed according to the standards by the Norwegian Institute of Marine Research. The sea lice monitoring is organised so that trained personnel count lice in the field using a headlamp. The fish was first sedated and counted for lice and then euthanized and sampled for gill tissue. *Lepeoptherius salmonis* lice were identified as chalimus 1, chalimus 2, pre-adult, adult male, adult female or copepodid; the number of Caligus spp. lice was also counted as described in Hamre et al. (2013).

2.3 | Gill Tissue Sampling

Dead fish were sampled for gill tissue using scissors serially sterilised in an immersion of bleach, distilled water and 90% ethanol. The sample was preserved in RNAlater (Sigma Aldrich), refrigerated and then frozen until samples were shipped to the laboratory for analysis (procedure described by Teffer and Miller 2019; Jeffries et al. 2021).

2.4 | Genetic Analysis

Twenty individuals from each of 17 locations were pooled and assayed for microbes (17 bacteria, 16 parasites and 14 viruses; Table 1) using the Biomark HD high throughput microfluidic qPCR instrument (Standard Biotools). Based on the results from the pooled data and geographical distribution, individual fish from eight of the sampling locations were analysed. The location for individual analysis was chosen based on two criteria: (1) keeping a latitudinal distribution of sampling locations and (2) choosing locations that were of interest due to their potential heavy loads of pathogens or unique pathogen diversity. These locations were Jarfjord, Talvik, Steigen, Etne, Ytre Årdalsfjord, Herøyosen, Hitra and Flekkefjord.

Total RNA were extracted from gill tissue by homogenisation of tissue in TRI reagent (Ambion Inc.) followed by aqueous separation using 1-bromo- 3-chloropropane. Resulting supernatants were used to extract purified total RNA using the Magmax-96 for Microarrays RNA Kit (Ambion Inc.) on a Biomek NXP (Beckman-coulter) automated liquid handler according to the manufacturer's 'spin method'. Extracted RNA (1.0 μg) was reverse transcribed to cDNA using the SuperScript VILO Master Mix Kit (Invitrogen) following the manufacturer's method. The BioMark platform employs nanofluidics, as per manufacturer's recommendations, and specific target amplification (STA) of assays is required (Dhoubhadel et al. 2014). The cDNA (1.3 μL) from each sample was preamplified with a mixture of 0.2 μM primer pairs for each of the assays applied in a given dynamic array run using TaqMan Preamp MasterMix (Applied Biosystems) in a 5 μL reaction. The preamplification was run for 14 amplification cycles, as per the BioMark protocol. ExoSAP enzyme treatment (Affymetrix) was used to remove unincorporated primers from the assays, which were then diluted 1:5 in DNA Suspension Buffer (Teknova). For pathogen quantification, artificial positive constructs (APC) were created from each microbe assay region's sequence, with an additional sequence added that allowed for the detection of vector contamination (see Miller et al. 2016). A serial dilution of these APC clones was run on the dynamic array for calculation of assay efficiency as well as determination of copy number for detected microbes. BioMark Fluidigm Dynamic Arrays were run according to the manufacturer's instructions. Cycle threshold (CT) values were determined using the Fluidigm Real-Time PCR analysis software (Standard Biotools).

2.5 | Fish Farming Intensity

The density of farmed fish was extracted from the report of impacts of salmon louse on wild salmon assessed yearly in the traffic light systems. The reports are in Norwegian and can be found online (https://trafikklyssystemet.no/), and the report from 2023 includes a table of the number of farmed fish per km^2 in each production area. These data are based on the reported number of farmed fish to the Norwegian Directorate of Fisheries. The km^2 per production area is based on the sea area inside the baseline of Norwegian territorial sea. The data are presented as an average number across 2-year periods and the average across 2021 and 2022 was extracted and used as a coarse estimate of density of farmed fish for the different sampling locations.

2.6 | Data and Statistical Analysis

Individual samples were taken from 160 sea-run brown trout from eight regions within the NALO sampling territory, from southern Norway along the North Sea to the high north along the Barents Sea. Two hypothesis tests were conducted on the fish pathogens using permutated multivariate analysis of variance (perMANOVA) with either fish farm biomass or latitude as predictors; a perMANOVA was fitted for each model using the *adonis2* function in vegan (Oksanen et al. 2022). This analysis requires the removal of rows with zero sum, that is, fish in which no pathogens were detected. This was the case for five trout, two from Hitra, one from Talvik, one from Jarfjord and one from Heroyosen. To visualise the relationships, pathogen data from all fish were ordinated using non-metric multidimensional scaling, a tool for data reduction of biodiversity sampling (see Teffer et al. 2017). Ordination was conducted on 47 pathogens, 27 of which were not detected at all in the sample. Both axes of the NMDS were plotted and additional information about the lice infestation of the fish was ordinated onto the axes using the *envfit* function in vegan (see Teffer et al. 2017).

3 | Results

3.1 | Pooled Data

In total, 14 pathogens were detected across all the pooled samples (Figures 1 and 2). Notably, some of the pathogens

TABLE 1 | Assays run for microbes of type bacteria, virus and parasite.

Microbes	Type	Name_number	Description
Aeromonas salmonicida	Bacterium	ae_sal_12	
Renibacterium salmoninarum	Bacterium	re_sal_44	
Candidatus *Branchiomonas cysticola*	Bacterium	c_b_cys_13	Common bacteria in open cage salmon net pens, one of several causes of proliferative gill disease (Toenshoff et al. 2012); suggested to have a central role in Complex gill disease (Herrero et al. 2018).
Flavobacterium psychrophilum	Bacterium	fl_psy_18	Agent of bacterial cold water disease (BCWD) in freshwater reared salmonids (Holt 1987; Starliper 2011).
Moritella viscosa	Bacterium	mo_vis_28	
Pasteurella atlantica	Bacterium	pa_atl_479	
Piscichlamydia salmonis	Bacterium	pch_sal_39	Ubiquitous in freshwater and in the marine environment, but believed to have a low impact on the gill health of farmed salmonids in Norway (Boerlage et al. 2020)
Piscirickettsia salmonis	Bacterium	pisck_sal_40	A bacterium of marine origin described from affected farmed coho salmon in Chile (Fryer et al. 1990; Fryer and Hedrick 2003). Has been recorded affecting many salmonid species including farmed Atlantic salmon in Norway (Olsen et al. 1997).
Pasteurella skyensis	Bacterium	pa_sky_477	
Rickettsia-like organism (RLO) (Strawberry disease)	Bacterium	rlo_45	Pathogens of salmonids in many geographical regions where they are farmed including North America, South America and Europe (Branson and Nieto Diaz-Munoz 1991; Brocklebank et al. 1992; Grant et al. 1996; Olsen et al. 1997).
Candidatus Syngnamydia salmonis	Bacterium	sch_47	Bacteria known to be associated with complex (multi-agent) gill disease in farmed Atlantic salmon in Norway (Nylund et al. 2015).
Tenacibaculum dicentrarchi	Bacterium	te_dic_475	One of three Tenacibaculum species known to cause Tenacibaculosis in the marine environment (Avendaño-Herrera et al. 2016; Nowlan et al. 2021)
Tenacibaculum finnmarkense	Bacterium	te_fin_473	
Tenacibaculum maritimum	Bacterium	te_mar_51	Different species of Tenacibaculum spp. is known to cause the disease Tenacibaculosis in farmed Atlantic salmon (Nowlan et al. 2021). Among these, *T. maritimum* is considered as the most virulent in BC (Wade and Weber 2020). *Tenacibaculum finnmarkense* genomvar finnmarkense has been described as the primary cause of the disease in Norway, while infections with *T. maritimum* have occasionally been reported in association with gill diseases in farmed Atlantic salmon (Småge et al. 2016).
Vibrio anguillarum	Bacterium	vi_ang_55	
Vibrio salmonicida	Bacterium	vi_sal_56	

(Continues)

TABLE 1 | (Continued)

Microbes	Type	Name_number	Description
Yersinia ruckerii (Enteric redmouth disease)	Bacterium	ye_ruc_61	
Ichthyobodo salmonis	Parasite	Ic_spp _472	Euryhaline parasite detected in both wild and farmed hosts and associated with complex gill disease in marine salmonid farms (Isaksen et al. 2011)
Ichthyobodo necator	Parasite	Ic_spp _472	An *Ichthyobodo* species acquired in freshwater (Todal et al. 2004) associated with skin and gill disease in salmon and trout hatcheries (Isaksen et al. 2010)
Neoparamoeba perurans	Parasite/Amoeba	ne_per_32	
Ichthyophthirius multifiliis	Parasite/Ciliate, protozoan	ic_mul_21	Causative agent of white spot disease (Fouquet 1876) with widespread geographical distributions from tropical to temperate zones (Matthews 2005)
Spironucleus salmonicida (Diplomonadida; Hexamitidae); aka *Hexamita salmonis*	Parasite/Flagellate	sp_sal_49	
Sphaerothecum destruens	Parasite/ Mesomycetozoea	sp_des_48	
Loma salmonae (Loma spp.)	Parasite/ Microsporidian	lo_sal_27	Associated with Microsporidial Gill Disease of Salmon (MGDS) in farmed *Oncorhynchus* spp. in Canada (Magor 1987), and detected in farmed *Salmo* spp. in the United Kingdom (Poynton 1986). Not associated with severe disease outbreaks in salmon farms in Europe or yet detected in Norway.
Nucleospora salmonis	Parasite/ Microsporidian	nu_sal_33	Microsporidian most known to infect Pacific salmon; not studied in Norway. Infects the haematopoietic cells of salmonid fishes, can cause direct mortality but often leads to a chronic disease and immune suppression (Hedrick et al. 1990)
Paranucleospora theridion	Parasite/ Microsporidian	pa_ther_38	Synonym: *Desmozoon lepeophtheirii*. Complex life cycle with development stages in sea lice (*Lepeophtheirus salmonis*) and salmon (Nylund et al. 2011). Associated with complex gill diseases in Atlantic salmon (Nylund et al. 2011; Weli et al. 2017).
Kudoa thyrsites (Kudoa spp.)	Parasite/ Myxozoan	ku_thy_26	
Myxobolus arcticus	Parasite/ Myxozoan	my_arc_29	Identified host in N Europe (Norway, Iceland) is Arctic Char (*Salvelinus alpinus*). Infects tissue of CNS.
Parvicapsula pseudobranchicola	Parasite/ Myxozoan	pa_pse_37	Marine myxosporean parasite with complex life cycle (marine polychaete is probably the alternate host). Infections detected in farmed salmon and wild sea trout in Norway, particularly in the north (Nylund et al. 2005; Karlsbakk and Nylund 2007; Hansen et al. 2013).

(Continues)

TABLE 1 | (Continued)

Microbes	Type	Name_number	Description
Parvicapsula kabatai	Parasite/ Myxozoan	pa_kab_35	
Tetracapsuloides bryosalmonae	Parasite/ Myxozoan	te_bry_50	Myxozoan parasite with an alternate bryozoan host causing proliferative kidney disease associated with population-level impacts on wild salmon and trout (Clifton-Hadley and Feist 1989)
Parvicapsula minibicornis	Parasite/ Myxozoan	pa_min_36	
Cryptobia salmositica	Parasite/Protozoan	cr_sal_15	
Ichthyophonus hoferi	Parasite/Protozoan	ic_hof_20	Opportunistic fungus-like agent causes systemic disease in marine fish and is thought to transmit trophically (Hershberger et al. 2002; Bass et al. 2017). Found to induce chronic inflammatory disease in salmon (Deeg et al. 2022).
Atlantic salmon paramyxovirus (ASPV)	Virus	aspv_58	
Piscine myocarditis virus (PMCV)	Virus	pmcv_41	
Piscine orthoreovirus 1 (PRV1)	Virus	prv-1_42	Associated with heart and skeleton muscle inflammation (HSMI) in farmed Atlantic salmon in Norway (Kongtorp et al. 2004) and determined as the causative agent (Wessel et al. 2017). PRV-1 has also been detected in wild Atlantic salmon, but infections appear to be rare in sea trout (Garseth et al. 2013).
Infectious haematopoietic necrosis virus (IHNV)	Virus	ihnv_22	
Infectious pancreatic necrosis virus (IPNV)	Virus	ipnv_23	
Infectious salmon anaemia virus (ISAV)	Virus	isav_25	
Piscine orthoreovirus 3 (PRV3)	Virus	prv-3_474	Causative agent for HSMI-like disease in farmed rainbow trout. PRV-3 infections are more commonly detected in wild sea trout (*Salmo trutta*) than wild Atlantic salmon (Garseth et al. 2019)
Rota virus	Virus	p-rotav_454	
Salmon Gill Pox virus (SGPV)	Virus	sgpv_161	
Salmon alphavirus 1, 2 and 3 (SAV-PD/SD/HSS)	Virus	sav_46	
Putative Toti-like virus	Virus	p-totiv_164	
Erythrocytic necrosis virus (ENV)	Virus	env_52	
Viral encephalopathy and retinopathy virus (VER)	Virus	ver_53	
Viral haemorrhagic septicemia virus (VHSV)	Virus	vhsv_54	

Note: Two *Ichthyobodo* assays are listed here that were pooled for the analysis.

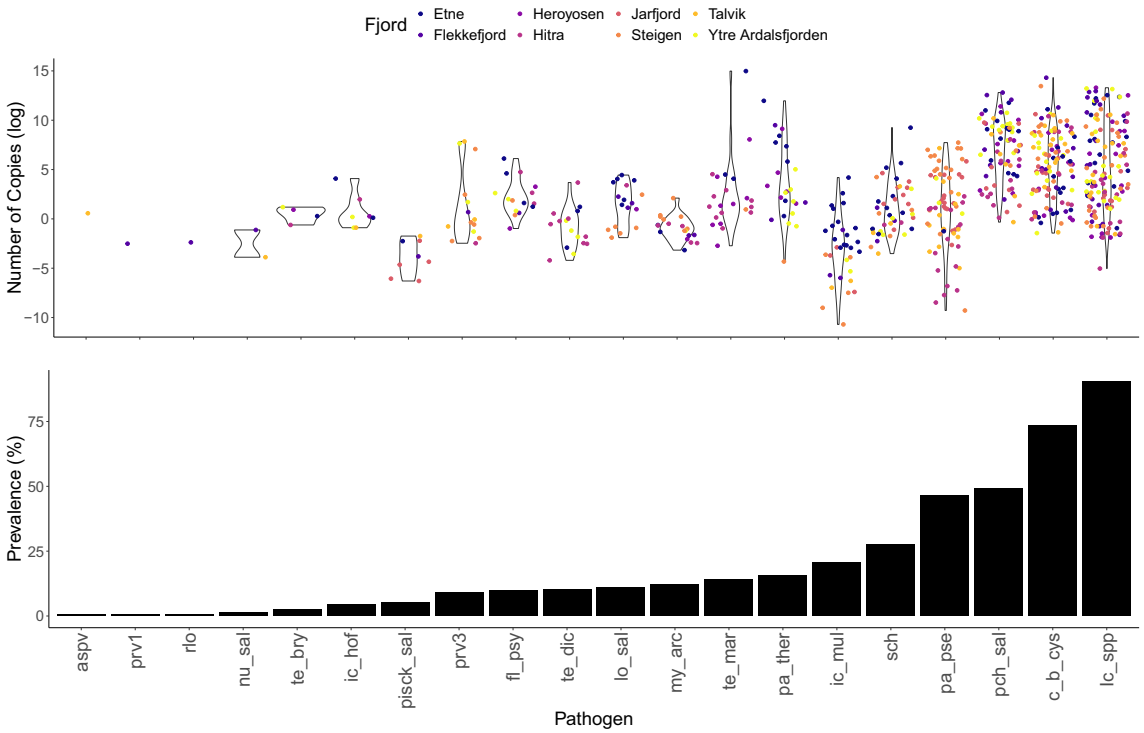

FIGURE 2 | Number of copies for each pathogen coloured by fjord (refer to Figure 1 for map) and overall prevalence of pathogens within the sample. Pathogen keys can be found in Table 1.

were ubiquitous across these sampling locations. These were *Branchiomonus cysticola* and *Ichthyobodo* Spp. Furthermore, *Piscichlamydia salmonis* was detected at all locations except for in the northern location Oksfjorden. Two pathogens displayed a clear north to south gradient, *Paranucleospora theridion* (aka *Desmozooan lephthiopterae*) was only detected at the southern locations, whereas *Parvicapsula pseudobranchicola* was abundant in the northern sites, but only seldomly detected in the south. Other notable detections were the first detections of *Loma salmonae* at multiple locations, with a trend towards more frequent detections in the south. This is the first detection of this pathogen in Norwegian salmon and warrants further investigation and sequencing. The diversity of pathogens did not vary significantly across latitudes, although there was a tendency that locations in the southwestern Norway had higher number of detected pathogens ($n = 6–9$) compared to in other locations, and that the locations with the fewest pathogens were in the northern sampling areas (e.g., Oksfjord, $n = 4$).

3.2 | Individual Data

One hundred and sixty individual sea-run brown trout from eight systems in Norway were screened, five of which were excluded due to having no pathogens detected (note: we did not exclude them to manipulate the data, but because non-metric multidimensional scaling will not fit with rows having zero sums). Fish farm biomass extracted from the production areas provided a general latitudinal increase in production from the north towards the farming hotspots in western Norway to the region of Etne, and further south a general decrease to the region of Flekkefjord (i.e., non-linear latitudinal trend); however, there was not strong evidence that the variation in pathogen diversity was related to the fish farming density ($F = 0.92$, $p = 0.55$). Permuted multivariate analysis of variance did, however, indicate that latitude was significantly related to the pathogen community ($F = 4.04$, $p < 0.01$; Figure 3). Ordination of the sea lice data (Figure 4) using *envfit* provided a significant association between pathogen diversity and copepodid stage of the louse species *Lepeophtheirus salmonis* ($p = 0.03$).

4 | Discussion

High-throughput pathogen profiling (Miller et al. 2016) was conducted on gill samples of sea-run brown trout samples from systems ranging from the North Sea in southern Norway to the Norwegian and Barents seas in the high north of Norway. Sampling covered much (about half) of the native European distribution of sea-run brown trout and included most of the area where populations are in relatively good status compared to southern parts of the distribution in Portugal, Spain and France. Pathobiomes of fish from these trout populations were characterised and contrasted with a broad-scale approach for the first time, identifying latitudinal variation in the presence and abundance of key pathogenic species and limited evidence that pathogen diversity was related to intensity of fish farming.

Several biogeographic rules exist to explain or predict the diversity of species (including pathogens) at northern latitudes. In general, species richness is expected to decline at northern latitudes (Hillebrand 2004). Although our latitudinal cline covered

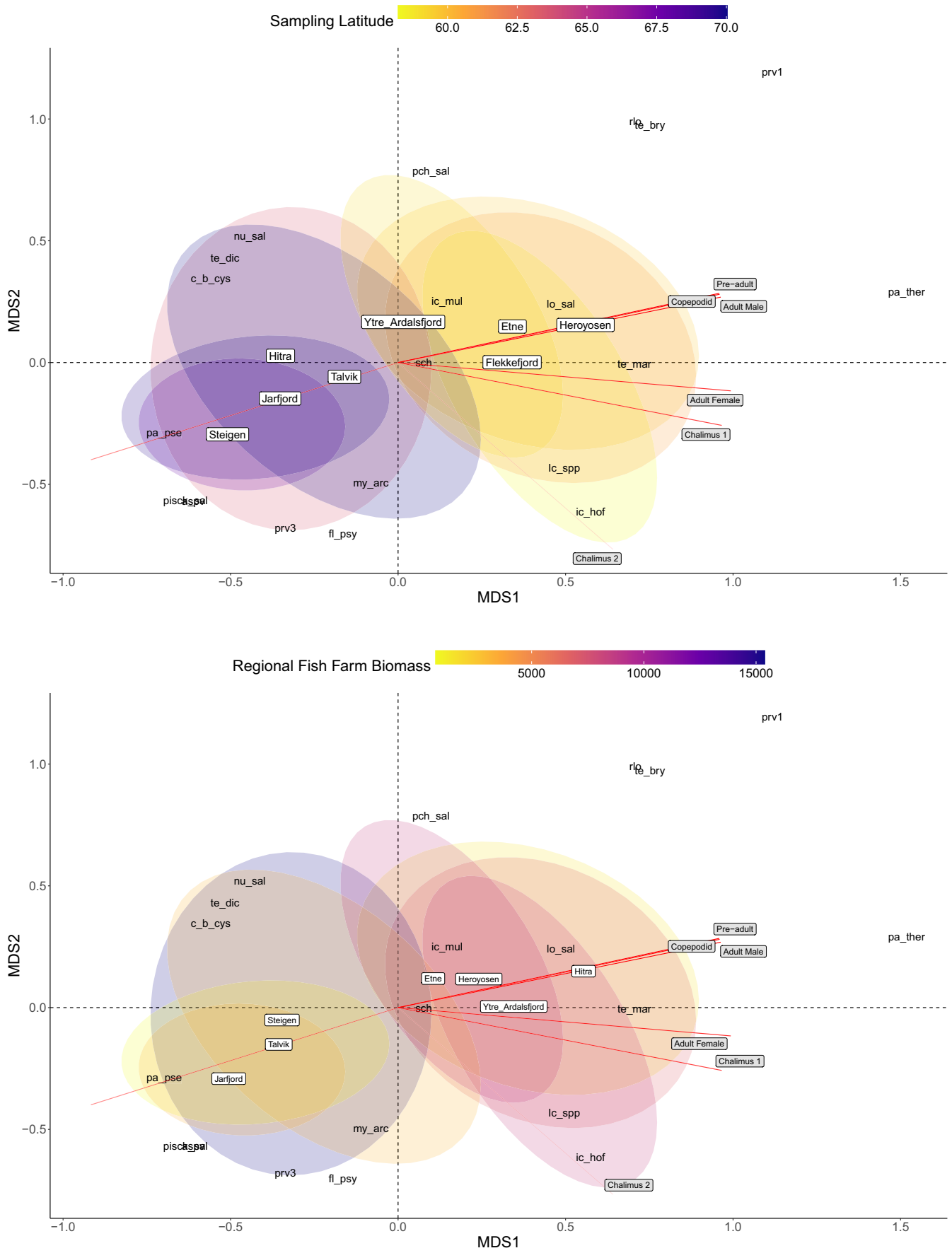

FIGURE 3 | Legend on next page.

FIGURE 3 | Non-metric multidimensional scaling ordination of pathogens (log copy numbers) from the latitudinal sampling of sea-run brown trout. Trout were sampled as part of the National Sea Lice Monitoring Program in spring 2020–2022. Fifty per cent ellipses are drawn for each production area in Norway according to where the samples were taken (included as black and white labels), and coloured by fish farming biomass in that production area in 2021. Sea lice counts for individuals were also included as black and grey labels with placement according to ordination with the *envfit* function in R vegan; red segments indicate the strength of the relationship where copepodid stage was the only significant lice stage according to *envfit* (Oksanen et al. 2022).

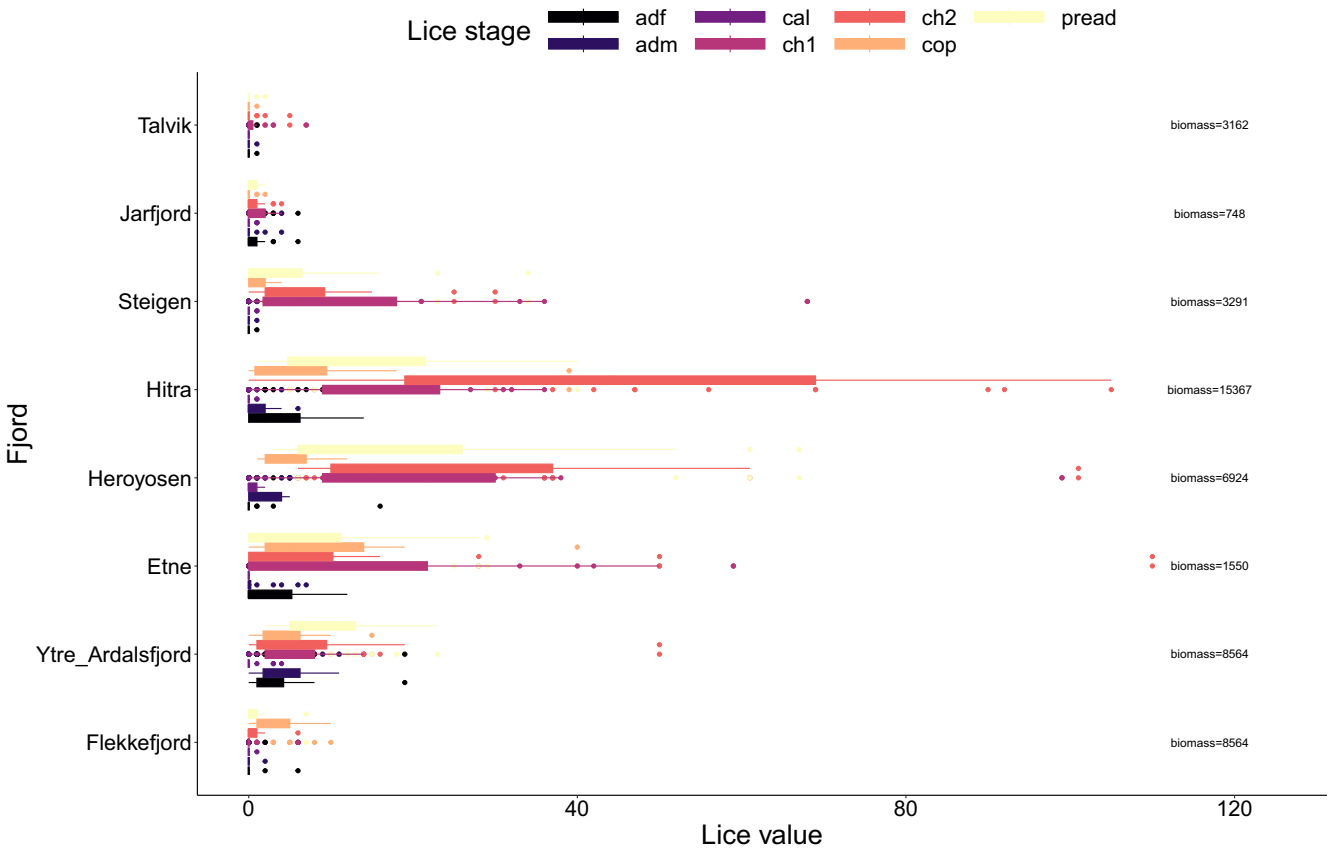

FIGURE 4 | Lice counts on sampled sea-run brown trout from the eight fjord systems in Norway. Colours indicate the life stages of lice, including chalimus 1 (ch1), chalimus 2 (ch2), pre-adult (pread) and copepodid (cop). For cross-reference, the fish farm biomass in the regional production area is provided on the right margin of the figure.

only about 13° of latitude from southern to northern Norway, this is an area across which pathogen biodiversity should be reasonably expected to shift; in the northern regions of our study area, Jarfjord to Steigen, the fjords are characterised by colder temperatures and seasonal darkness; sea-run brown trout residing in these areas may have shorter marine feeding phases than in southern areas that would affect the life cycle of several pathogenic species. Taken together, it was reasonable to predict lower diversity of fish pathogens at northern latitudes. Although there were not extreme shifts in pathogen biodiversity across latitudes and most species were present to some degree across all trout populations, there was evidence that biodiversity metrics were linked to a latitudinal gradient with lower diversity in the north.

Humans have exerted an extreme influence on biogeography around the world by moving species and altering the habitats available to species, driving both local increases and decreases in biodiversity indicators (e.g., Capinha et al. 2015). Anthropogenic climate change is a way in which humans are influencing biogeography at a broad scale (Ackerly et al. 2010). In addition, the movement of animals, especially migratory species like brown trout, will redistribute pathogens within the environment (Smith 2009). Fish farming has started to pervade most of Norway; as one of the country's largest industries, fish farming has been established in nearly every suitable area of the sea from southern to northern Norway. We did not find that the pathobiome richness of sea-run brown trout was related to the regional density of fish farming. There were hotspots in the pathobiome diversity and relative infective burdens in fjords of western Norway where farming is most intense (e.g., in Etne, where there appears to have been an epizootic outbreak of *T. maritimum* infection), a deviation in the linearity of the latitudinal slope suggesting that climate was not necessarily the only regulator of the pathobiome. A reason for the lack of effect of fish farming intensity could therefore be linked to that the effect

of farming is on a more local scale. Whereas there are lower densities of farms in Northern Norway, farms do indeed exist, so any potential introductions of agents common on farms, and perhaps not historically in wild salmon and trout, is likely to have already occurred.

Interestingly, there was an association between the copepodid levels of sea lice on individual sea-run brown trout and the pathogen composition as described in the NMDS analysis. This could indicate that individual sea-run trout within sample location had been exposed to a varying degree of infestation pressure from fish farms. As well, it is also possible that sea lice may serve as transmission vectors of salmon pathogens and/or may increase susceptibility to pathogen infection/disease. Studies implicating sea lice as a potential transmission vector for salmon viruses (e.g., ISAV [Oelckers et al. 2014], IHNV [Jakob, Barker, and Garver 2011], piscine orthoreovirus [Mordecai et al. 2019]), microparasites (e.g., *Paranucleospora theridion* [Økland 2012]) and bacterial agents (e.g., *Tenacibaculum* spp., *Moritella viscosa* and *Vibrio spp.*[all three–Morales-Rivera et al. 2022; Valenzuela-Miranda et al. 2024]) are expanding with the advent of next generation sequencing. Many of these agents are either known to infect blood (e.g., PRV, ISAV) or skin/gill tissue (all of the bacterial and parasitic agents identified in sea lice) of salmon, which would explain how these agents may be transmitted to and from sea lice. There is also a growing literature implicating sea lice infections in enhanced susceptibility to secondary infections generally (Valenzuela-Miranda et al. 2024), and for specific agents, (e.g., ISAV [Brooks 2005; Barker et al. 2019], and *Piscirickettsia salmonis* [Lhorente et al. 2014]). Given that sea lice can disrupt the integrity of the skin, even if sea lice are not a direct transmission vector, it is likely that opportunistic ecto-parasites and bacteria, like *Tenacibaculum* spp. and *Moritella viscosa*, will carry enhanced infection and disease causing potential in fish infected with sea lice. For example, laboratory challenge studies have found that *Tenacibaculum* spp. infections become more virulent when skin/gill tissue is abraded (Powell et al. 2005). Consistent with these findings in the literature, the two agents that showed strongest positive associations with copepodid levels of sea lice on migratory sea-run brown trout, *T. maritimum* and *P. theridion*, are both known to be carried by sea lice. Like sea lice, these agents are also positively associated with water temperature (Avendaño-Herrera, Toranzo, and Magariños 2006; Gunnarsson et al. 2017); hence, they may become more problematic as the climate warms. As a result, a precautionary approach projecting forward is warranted in the intensification of farms in northern regions of Norway, with continued control of sea lice and monitoring of these and other agents.

Salmon pathogens most closely associated with northern regions of Norway largely include agents that are considered natural pathogens of trout (e.g., *Piscirickettsia salmonis*, *Parvicapsula pseudobranchicola, Nucleospora salmonis*, to a lesser degree, PRV-3), rather than being specifically increased on Atlantic salmon farms. While *P. salmonis* can infect and cause disease in farmed Atlantic salmon (Olsen et al. 1997), its impact has been severely diminished on farms in Norway possibly due to better smolt quality/husbandry (Rozas and Enríquez 2014), but is still considered one of the most important threats to the salmon farming industry in Chile (Rozas and Enríquez 2014). In both Norway and Chile, *P. salmonis* is highly impactful on trout farms (Fryer and Hedrick 2003; Rozas and Enríquez 2014), as well as coho (*O. kisutch*) salmon farms in Chile. Moreover, sea-run brown trout and *Oncorhynchus* species are considered a more natural host for *P. pseudobranchicola*, and *N. salmonis* than Atlantic salmon (Hansen et al. 2015; Jones, Low, and Goodall 2023; El Alaoui, Grésoviac, and Vivarès 2006). PRV-3 is well established as a pathogen of trout (Vendramin et al. 2019), and has routinely been detected in surveys of sea-run brown trout (Garseth et al. 2019).

High-throughput microfluidics approaches now allow broad-scale screening for pathogens rather than targeted assessments of single-species assays that are more typically applied to identify pathogens of interest (Miller et al. 2014, 2016). Screening programmes are often included as part of surveillance efforts for a specific pathogen of interest or as a reaction to an outbreak at a farm, which creates gaps and biases in the understanding of the pathobiome that can be overcome with replicated sampling as we conducted here. We focused specifically on the early marine migration of brown trout by coordinating sampling with the national sea-lice surveillance programme that takes place during spring months throughout Norway, which makes these data a snapshot of pathogens during a specific phase of the sea-run brown trout's life. Seasonality has an important influence on infectious disease and impact (Altizer et al. 2006; Bass et al. 2019), and these sea-run brown trout would likely spend several weeks or months in the fjords before the survivors return to rivers during July–September before spawning in ~October. In the months following sampling, they would likely contract new pathogens or experience an increased burden of their existing pathobiome leading to disease and perhaps death or other fitness consequences.

Studies linking the pathobiome to end points are rare in field settings and there may be latitudinal gradients in immunocompetence that are important but not studied here. Fish experiencing the burden of a pathogenic infection may upregulate immunity-related genes to fight the infection and reduce the potential for the pathogen to replicate and cause disease. In this study, we did not measure gene expression to evaluate whether such genes were upregulated, or conduct histopathology to determine if there was any evidence of disease. Diversity in the major histocompatibility complex will additionally play a role in immunity and previous research on Atlantic salmon in Canada has indicated that low diversity of MHC complexes in northern populations of salmon underlies a trade-off by fish in the north where there is lower disease risk. Our data did not resolve a strong pattern of reduced pathogen richness in northern Norway, where they salmon farming industry is only beginning to expand, nor did our data reveal a significant effect of farm biomass; however, we did reveal a differential distribution of pathogens between southern and central compared to northern Norway, which was significantly correlated with production area measurements of copepodid sea lice. Importantly, the agents most closely associated with sea lice and farm activity—namely *T. maritimum* and *P. theridion*—are known to be carried by sea lice. In northern Norway, sea-run brown trout were more commonly infected with agents known to infect and cause disease in trout, consistent with lower transmission risks from Atlantic salmon farms in the north. It is also possible that farm-based disease risks may be lower in the north due to lower temperatures; two of the agents driving variation between southern and central Norway and northern Norway are

known to respond positively to temperature. More research on the role of climate change on infectious disease risk (e.g., Altizer et al. 2013) including specific to fish (Marcogliese 2008) is potentially warranted to determine whether climate plays a key role in immunity that will cause northern populations to become immunocompromised where warming is having an effect.

Author Contributions

Project was conceived by Lennox, Vollset, Miller, and Madhun. Data were collected by Vollset, Eldoy, and Nilsen. Funding was awarded to Vollset, Lennox, Miller, Madhun, and Davidsen. Laboratory work was completed by Schulze and Miller. Analysis was conducted by Lennox. All authors contributed to writing and editing.

Acknowledgements

A simulation was performed to determine who would be first and last author on the paper between RJL and KWV using the *sample* function in R, who contributed equally to funding acquisition, experimental design and manuscript writing. This research was funded mainly by the NFR project PACE (Pr. nr. 303301). Dylan Shea and Trond Einar Isaksen were financed by PATHDNA (Pr.nr. 326900). KMM provided the high throughput molecular technology and contributed substantially to interpretation and writing. We thank Dr. Art Bass for assistance with figure coding. Fish sampling was permitted by the Norwegian Environmental Directorate as part of the NALO program (document 2020/2710).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are available on github at github.com/robertlennox/BTN and can be opened in R by running: BTN::pace.

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