Received: 16 March 2024 | Revised: 10 June 2024 | Accepted: 13 June 2024

DOI: 10.1111/jfd.13990

RESEARCH ARTICLE

Journal of Fish Diseases WILEY

First detection of *Ichthyophonus* sp. in invasive wild pink salmon (*Oncorhynchus gorbuscha*) from the North Atlantic Ocean

Toni Erkinharju | **Haakon Hansen** | **Åse Helen Garseth**

The Norwegian Veterinary Institute, Ås, Norway

Correspondence
Åse Helen Garseth, The Norwegian Veterinary Institute, Elizabeth Stephansens vei 1, Ås 1433, Norway.
Email: ase-helen.garseth@vetinst.no

Abstract

Pacific pink salmon (*Oncorhynchus gorbuscha*) were deliberately introduced to rivers surrounding the White Sea and has spread to Norway and several other countries surrounding the North Atlantic Ocean. In August 2021, a female pink salmon displaying pale gills and abnormal behaviour was captured in River Lakselva in Northern Norway and later submitted to the Norwegian Veterinary Institute (NVI) for post-mortem examination. Histological examination of organ samples revealed structures indicative of systemic ichthyophoniasis, caused by *Ichthyophonus* sp. The parasites appeared to be especially abundant in the heart and skeletal musculature, and local tissue responses were assessed to be absent or very mild. Sequences of the ribosomal 18S rRNA and the mitochondrial cytochrome oxidase 1 (CO1) genes confirmed the diagnosis and identified the pathogen as *Ichthyophonus* sp. The CO1 sequence further established that the isolate from pink salmon was most similar to sequences of *Ichthyophonus* sp. from Atlantic salmon, *Salmo salar*, from the Atlantic Ocean on the east coast of the US and from Atlantic herring, *Clupea harengus*, from Iceland. We here report the first detection of *Ichthyophonus* sp. in pink salmon in the North Atlantic Ocean.

KEYWORDS
Ichthyophonus sp., invasive species, *Oncorhynchus gorbuscha*, parasite, pink salmon, wild

1 | INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) are native to the Pacific Ocean but were deliberately released to rivers surrounding the White Sea in Russia during the two periods 1956–1979 and 1985–2000 (reviewed by Hindar et al., 2020). Secondary spread of this invasive species has resulted in pink salmon runs in rivers in Norway and other countries surrounding the North Atlantic Ocean (Armstrong et al., 2018; Eliasen & Johannesen, 2021; Millane et al., 2019; Nielsen et al., 2020; Sandlund et al., 2019; Skóra et al., 2024). Introduction and spread of pathogens are identified as potential risks associated with pink salmon invasions (Armstrong et al., 2018; Hindar et al., 2020; Lennox et al., 2023; Millane et al., 2019; Sandlund et al., 2019). Accordingly, the Norwegian Veterinary Institute (NVI) has organized health monitoring of pink salmon in Norway since 2019, including risk-based surveillance, that is, based on examination of pink salmon with signs of disease.

Parasites in the genus *Ichthyophonus* (Ichthyosporea) are ubiquitous in the marine and freshwater environment and cause systemic disease in a number of finfish species. To date, only

two species, *Ichthyophonus hoferi* (Plehn & Mulsow, 1911) from rainbow trout and *I. irregularis* (Rand et al., 2000) from yellowtail flounder *Myzopsetta ferruginea*, have been formally described. However, more recent genetic data suggest the presence of several species within the genus (Gregg et al., 2016, 2022; Hershberger et al., 2016; Rasmussen et al., 2010), but there is no consensus on how to delimit species within the genus with molecular tools. Rasmussen et al. (2010) and Gregg et al. (2016) analysed sequences of the ribosomal internal transcribed spacer from several isolates to resolve species, but with limited success. Recently, Gregg et al. (2022) analysed sequences of the mitochondrial cytochrome oxidase 1 gene and demonstrated clear lineage separation between marine isolates of *Ichthyophonus* sp. showing that this could be a promising tool as a species identifying marker. Systemic infections with *Ichthyophonus* sp. can be subclinical or manifest as a wide range of disease signs including abnormal behaviour, ulcerations, pale gills and mass mortality (Jones, 2013). While a high proportion of pink salmon from the Gulf of Alaska in the North Pacific have been reported to be PCR-positive for *Ichthyophonus hoferi* (Deeg et al., 2022), the parasite has not been found in this species in the Atlantic although a few investigations have been carried out, both in the White Sea and Barents Sea (Barskaya et al., 2005; Grozdilova, 1974; Ieshko et al., 2016; Ninburg, 1963; Sokolov et al., 2024) and in Norwegian waters (Fjær, 2019; Rullestad, 2021). Here we report on the first detection of *Ichthyophonus* sp. in an invasive pink salmon captured in a Norwegian river and also for the first time describe histopathological findings in this host.

2 | MATERIALS AND METHODS

2.1 | Study sample

The studied pink salmon was captured on August 2021 in River Lakselva (Norwegian Water course code 224.Z, 70°04′45.7″N 24°55′33.1″E), which is a National Salmon River situated in Porsanger in the County of Finnmark (Data S1). The 400 km long river originates in Karasjok and drains to the Porsanger fjord and holds a naturally large population of Atlantic salmon *Salmo salar* (spawning target 3424 kg females). In addition, the river holds populations of anadromous Arctic char, *Salvelinus alpinus*, sea trout, *Salmo trutta*, and grayling, *Thymallus thymallus*. In 2021, altogether 110,549 pink salmon were removed from 46 rivers in the Counties Troms and Finnmark, and 1028 of these were removed from River Lakselv (Anon., 2022).

The studied pink salmon was captured because it behaved abnormally and therefore attracted attention from the local river ranger. In contrast to the vigorous and aggressive behaviour of the pre-spawning pink salmon schooling in the midst of the river, this female specimen was lethargic, unaccompanied and was observed near the riverbanks. The fish was laying with the ventral side upward, seemingly dead, but turned and attempted to swim away when the river ranger approached. The pink salmon was easy to catch, and besides the described abnormal behaviour, the gills were pale, while the nutritional status was normal to good (i.e., high condition factor) (Data S2). The river ranger killed the pink salmon and stored it in a local freezer at −20°C. More than 1 year later, in September 2022, the pink salmon was submitted to NVI for examination.

2.2 | Post-mortem examination and histopathology

The pink salmon carcass was frozen on arrival at NVI on 6th September 2022. After thawing, the carcass was subjected to a routine necropsy procedure with recording of gross external and internal pathological changes. Tissue samples from gills, pyloric caeca, pancreas, liver, kidney, heart, skin and skeletal musculature were fixed in 10% neutral buffered formaldehyde (Sigma-Aldrich) for histopathological examination. After fixation, the tissue samples were routinely processed in accordance with Suvarna et al. (2019), including dehydration steps in alcohol, embedding in paraffin wax, sectioning to 2 µm thick samples and staining with haematoxylin and eosin (H&E), Gram and periodic acid–Schiff (PAS). Slides were scanned in a Hamamatsu NanoZoomer S360 and visualized using the software program NDP.view.2.7.25.0 (Hamamatsu Photonics K.K.).

2.3 | Molecular analyses

Tissue samples for PCR assays were taken from the kidney, myocardium, skin, brain and gill and transferred to 2 mL Eppendorf tubes filled with 1.5 mL RNAlater™. DNA was extracted using the DNEasyKit (Qiagen) on a QiaCube automatic extraction machine (Qiagen) following the manufacturer's instructions. Two different primer sets, Ich7f/Ich6r (Whipps et al., 2006) and GO1/Ich2R, (Criscione et al., 2002; Saunders & Kraft, 1994), were used to amplify two non-overlapping fragments of 371 and 661 bp of the ribosomal 18S rRNA gene. The annealing temperatures used in the PCR protocols for the two primer sets were 46 and 57°C, respectively.

In addition, a fragment of the mitochondrial cytochrome oxidase 1 (CO1) gene was amplified by PCR and sequenced. PCR primers were designed with Geneious Prime® (Ver. 2023.0.1) based on an alignment of all available CO1 sequences in GenBank (Date 1 April 2024) submitted as originating from *Ichthyophonus* sp. The primers Iphonus_CO1_F_HH (5'–TGAACTAATGAGCCGCGAAT–3') and Iphonus_CO1_R_HH (5'–AGTCTGGTATTCTACGAGGCA–3') were designed in conserved regions to amplify a 1378 bp fragment (including primers). The annealing temperature used in the PCR protocol was 55°C.

Amplicons were sequenced on the 3500xl Genetic Analyzer (Thermo Fisher Scientific) sequencer and proofread in Geneious Prime®. The resulting 18S sequences were then compared with sequences in GenBank through a BlastN search (Zhang et al., 2000). The CO1 sequence was aligned to the available sequences from GenBank, the alignment is cut to the length of the obtained proofread sequence, and the number of nucleotide differences was calculated in MEGA X (Kumar et al., 2018).

2.4 | Microbiology

Kidney tissue was harvested aseptically and inoculated by streaking on several growth media for bacteria (incubation temperature in parenthesis) including blood agar (BA) (22°C), blood agar with 2% NaCl (BAS) (15°C), kidney disease medium (KDM) (15°C), Anacker-Ordal (15°C), Kings Agar B (22°C) and Middlebrook 7H10 agar (22°C).

Tissue samples for detection of cultivable virus were harvested from kidney, myocardium, skin, brain and gill and transferred to virus-transport medium supplied by the NVI section for substrate production and logistics. The selected cell lines were an in-house epithelial cell line established from Atlantic salmon skin, bluegill fry cells (BF-2), epithelioma papulosum cyprini cells (EPC), chum salmon heart cells (CHH-1) and Atlantic salmon gill cells (ASG-10). Further processing of the samples was as described by Garseth and co-workers (2023).

3 | RESULTS

3.1 | Post-mortem examination and histopathology

At gross external examination (Data S2), the affected female pink salmon had a good nutritional condition and pale gills. Both of these characteristics were in line with the observations made by the river ranger. Accordingly, it is likely that the pale gills occurred antemortem and not merely because of post-mortem changes. The abdominal cavity was filled with loose eggs (roe), indicating that the pink salmon was ready to spawn. The freeze–thaw process had affected the carcass, but there were no further remarks from gross necropsy such as observations of ulcerations, or changes in texture or appearance of musculature, myocardium, liver or other internal organs.

As could be expected, histopathological examination revealed post-mortem autolysis and freezing artefacts. However, multiple fungal-like, variably sized parasitic structures resembling *Ichthyophonus* spp. resting spores and germinating bodies (as described in Bruno et al., 2006) were observed in a number of organs, several of which stained positively with the PAS stain (Figure 1). The size of the spores varied from 7 to 110 µm (average 41.6 µm, $n = 40$).

In the heart, tentative *Ichthyophonus* spp. were observed either as singular structures or clustered and appeared more abundant in stratum compactum than in stratum spongiosum of the ventricle. A few parasitic structures were also observed in the epicardium and the atrium of the heart. In general, inflammatory tissue responses were not observed, except a possible fibrinous myocarditis associated with parasites in the stratum spongiosum. In some of the parasitic structures, germination was observed (Figure 1b–g).

Multifocal *Ichthyophonus* sp. were also observed in the skeletal musculature, generally without obvious signs of local tissue response. Possible exceptions were a few focal areas with myositis and/or fibrosis in red and white muscle (Figure 1c). The parasitic structures were especially abundant in both red and white musculature, but also present in dermis (Figure 1d) and in subcutaneous and intermuscular adipose tissue.

Advanced post-mortem changes with loss of most of the organ structure were observed in kidney, liver, gills, pancreas and intestines. However, few to several multifocal *Ichthyophonus*-like structures were also noted, such as within gill lamellae (Figure 1f) and in the mural parts of pyloric caeca (Figure 1e). A possible inflammatory tissue response associated with the parasite was observed in the liver, manifested as focal hepatitis.

3.2 | Molecular analyses

Positive PCR amplifications for ribosomal 18S and mitochondrial CO1 were obtained for samples from the skin, gill and myocardium. After DNA sequencing and proofreading, the resulting non-overlapping sequences of the ribosomal 18S were 368 and 629 bps, respectively. The sequences are submitted to GenBank under accession numbers OR529304 and OR529305. No sequence variation was observed between sequences originating from different tissues. A BlastN search (updated 11 March 2024) for each of the obtained 18S fragments separately gave 99%–100% similarity to several sequences in GenBank, both labelled as *I. hoferi* or *Ichthyophonus* sp. and originating from different locations and hosts (see Data S3).

Due to poor sequence quality in each end of the obtained CO1 sequence, this sequence and thus the resulting alignment including 32 CO1 sequences, were cut to a length of 1127 bp (Supplementary 4). The CO1 sequence from pink salmon is deposited in GenBank under accession number PP883106. The alignment and subsequent calculation of genetic distances (*n* differences) found the sequence to be most similar, and only one nucleotide different, from two different isolates originating from Atlantic salmon from the Atlantic Ocean on the east coast of the US (Data S5). Isolates from Atlantic herring, *Clupea harengus*, from Iceland were the second closest being two nucleotides different from our isolate. Both the sequences from Atlantic salmon and Atlantic herring, and thus our sequence from pink salmon, further belong to a larger clade consisting of isolates from both the Atlantic and Pacific Ocean and from different host (Clade A, see Gregg et al., 2022, Figure 1 and Data S5 in this article). As there is a discussion whether *Ichthyophonus* spp. is one cosmopolitan species or a species complex (see, e.g., Gregg et al., 2022), and the fact that there is no consensus how to delimit species within the genus with molecular tools, we report our finding as *Ichthyophonus* sp.

3.3 | Microbiological examination

Bacteriological examinations were negative, and cultivable virus was not detected on the inoculated cell lines.

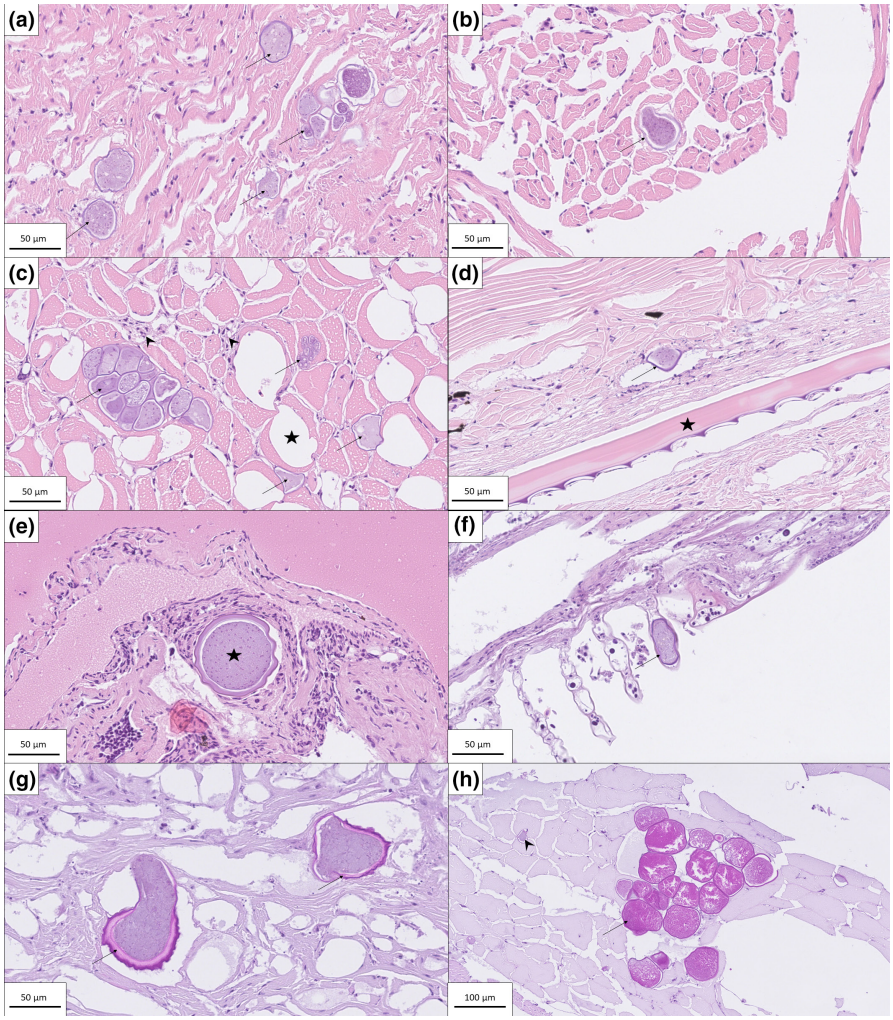

FIGURE 1 Histologic images of different tissues infected with *Ichthyophonus* sp. stained with H&E (a–f) and PAS (g–h). (a) Outer compact layer of heart ventricle with several basophilic, circular, double-walled and multinucleated structures in the myocardium (arrows), which are "resting spores" of *Ichthyophonus* sp. (b) Inner spongious layer of heart ventricle showing a single germinating spore in the myocardium (arrow) with a hyphae about to protrude through the outer spore wall. (c) Skeletal musculature with several resting spores, either singular or arranged into clusters (arrows). Possible mild inflammation or fibrosis (arrowheads) is noted. Several clear spaces within muscle cells (star) are also observed, which are most likely freeze artefacts. (d) Dermal (middle) layer of skin with a single resting spore (arrow), located close to a scale pocket (star). (e) Pyloric caeca with a single resting spore (star) within the muscularis layers. (f) Gills with parts of a spore (arrow) located within a gill lamella. (g) Germinating spores within the compact layer of heart ventricle were the outer spore wall stains PAS-positive (arrows). (h) Several PAS-positively stained resting spores (arrow) within the skeletal musculature, while some are PAS-negative (arrowhead). Scale bars 50 µm (a–g) and 100 µm (h). Photomicrographs taken at 40× (a–g) and 20× (h) magnification.

4 | DISCUSSION

To our knowledge, this is the first report of systemic *Ichthyophonus* sp. infection in pink salmon in the North Atlantic Ocean and the first supplemented with a histopathological description of ichthyophoniasis in this host species. Deeg et al. (2022) previously reported *I. hoferi* to be prevalent in pink salmon and three other salmonid species in the Gulf of Alaska by the use of high-throughput qPCR but did not include histopathological descriptions for pink salmon. There is a discussion whether *Ichthyophonus* spp. is one cosmopolitan species or a species complex and as there is no consensus on the molecular delimitation of species, we therefore report our finding as *Ichthyophonus* sp. It is however interesting to note that the CO1 sequences that are most similar to our CO1 sequence from pink salmon all come from isolates from fish hosts in the Atlantic Ocean. It is clear from the study of Gregg et al. (2022) and the genetic distances presented herein (Data S4) that the genus *Ichthyophonus* is deeply diverged and likely consists of several species. However, as some sequences retrieved from GenBank are from unpublished studies from other authors, we are not analysing or commenting further on this here.

In the specimen examined in this investigation, the parasite was observed in histological sections across several organs but appeared to be most abundant in the heart and skeletal muscle. This observation aligns with earlier findings indicating the parasite's preference for active musculature, particularly the cardiac muscle

in salmonids (Kocan et al., 2006). Interestingly, the parasite can also infect the brain in clupeid fishes, possibly inducing abnormal behaviour similar to that observed for the pink salmon in this case study (Marty et al., 1998; Rahimian & Thulin, 1996). Unfortunately, histological samples from the brain were unavailable for analysis, and molecular analyses of brain tissue yielded negative results for *Ichthyophonus* sp.

In general, an inflammatory tissue response to the presence of parasitic structures was absent or weak in the examined specimen in contrast to the strong, granulomatous inflammation with formation of whitish nodules often found in the heart, skeletal musculature and other organs of infected salmonids (Bruno et al., 2006). Although we only observed one infected specimen, it is not clear why our findings in this pink salmon are different from what is seen in other salmonids. In Chinook salmon, tissue response is visible upon gross inspection of organs and filets. According to Kocan and co-workers (2004), fish processors from Yukon River reported that as many as 20% of purchased fish (chinook salmon *Oncorhynchus tshawytscha*) were discarded because of damage to muscle tissue caused by *Ichthyophonus* sp.

Pink salmon that are removed from Norwegian fjords and rivers as part of the Norwegian control regime are considered as a source of fish meat for human consumption. It is therefore of general interest to assess whether infection with *Ichthyophonus* sp. has any implications for meat quality in pink salmon. In this diagnostic case, freezing and thawing of the carcass may have reduced the ability to identify gross visible nodules or altered texture attributable to the presence of *Ichthyophonus* sp. However, the general impression from histopathological investigation was that the tissue responses were sparse but not entirely absent. To date, NVI has performed post-mortem examinations of some hundreds of pink salmon and thus far not detected gross findings compatible with Ichthyophoniasis as described in Chinook salmon. However, a targeted survey of the prevalence and impact of the parasite, with gross, histopathological and PCR-based screening, has not been conducted, and thus, the prevalence and impact of *Ichthyophonus* sp. in pink salmon in Norway are therefore unknown.

Studies of Chinook salmon show a lower prevalence of *Ichthyophonus* sp. in female pink salmon at the spawning ground compared to female chinook in the main stem of the river (Kocan et al., 2004). This was interpreted as loss of infected females due to higher mortality during the migration upward the river. In addition, the prevalence of *Ichthyophonus* was also lower in females that had actually spawned compared to pre-spawning females. This could also be an indication of lower spawning success in infected female Chinook salmon (Kocan et al., 2004). The infected pink salmon examined in this case was ripe for spawning but clearly moribund and probably not able to complete spawning.

Ichthyophonus sp. is transmitted to piscivore fishes ingesting infected prey or by horizontal transmission (Kocan, 2019). Pink salmon perform long-distance migrations and can use large parts of the northeast Atlantic Ocean as feeding habitats (Armstrong et al., 2018; Diaz Pauli et al., 2022; Eliassen et al., 2021; Millane et al., 2019). Accordingly, they use the same feeding grounds as Norwegian spring-spawning herring *Clupea harengus* and mackerel *Scomber scombrus* (Utne et al., 2012). Studies have shown that 1% of herring and 50% of the mackerel captured in the same areas are infected with *Ichthyophonus* sp. (Storesund et al., 2022).

The invasive potential of pink salmon is partly due to their seemingly lower affinity to or homing to a specific river, and the source of infection is most probably infected prey ingested during the marine migration in the ocean. It is therefore not likely that Lakselv is more at risk than other rivers in this part of the country.

As the current study demonstrates that *Ichthyophonus* sp. was present in invasive pink salmon in Norway, we recommend that health surveillance and disease screening programmes include this group of parasites on the list of possible disease agents to gain more knowledge of the distribution of these parasites and the impact of Ichthyophoniasis on pink salmon in the Atlantic.

AUTHOR CONTRIBUTIONS

Toni Erkinharju: Investigation; validation; writing – review and editing; conceptualization; methodology; formal analysis. **Haakon Hansen:** Investigation; methodology; writing – review and editing; data curation; formal analysis. **Åse Helen Garseth:** Conceptualization; investigation; writing – original draft; project administration; writing – review and editing.

ACKNOWLEDGEMENTS

The authors would like to thank Martin Rognli Johansen from the Lakselva Landowner Association for submitting the infected pink salmon. Thanks also to Siw A. Larsen, Attila Tarpai and Saima Nasrin Mohammad at the Norwegian Veterinary Institute for performing their work with excellence. Finally, the authors thank the three reviewers whose comments contributed to the quality of the final manuscript.

FUNDING INFORMATION

The Norwegian Veterinary Institute financed the project.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GenBank (National library of medicine) at https://www.ncbi.nlm.nih.gov/genbank/, reference number OR529304 and OR529305.

ORCID

Toni Erkinharju https://orcid.org/0009-0001-3764-6011
Haakon Hansen https://orcid.org/0000-0003-1400-9615
Åse Helen Garseth https://orcid.org/0000-0002-8507-3246

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Erkinharju, T., Hansen, H., & Garseth, Å. H. (2024). First detection of *Ichthyophonus* sp. in invasive wild pink salmon (*Oncorhynchus gorbuscha*) from the North Atlantic Ocean. *Journal of Fish Diseases*, *00*, e13990. https://doi.org/10.1111/jfd.13990