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SHORT COMMUNICATION

High prevalence of *Ichthyophonus* sp. infections in Northeast Atlantic mackerel (*Scomber scombrus*)

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Ichthyophonus spp. are cosmopolitan parasites causing proliferative, systemic disease in a number of marine and freshwater fish, including several commercially important species such as Atlantic and Pacific herring (*Clupea harengus*, *C. pallasii*), rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*) (Gregg et al., 2016; Kocan et al., 2006; Rahimian & Thulin, 1996; Tierney & Farrell, 2004; Zuray et al., 2012). There is some uncertainty regarding both species diversity and host specificity within the *Ichthyophonus* genus, and at present only two species have been formally described, *I. hoferi* Plehn and Mulsow (1911) from rainbow trout and *I. irregularis* Rand et al., 2000 from yellowtail flounder (*Limanda ferruginea*). There are, however, strong genetic indications that the genus comprises more species than the two described so far (Hershberger et al., 2016; Rasmussen et al., 2010).

Atlantic mackerel (*Scomber scombrus*) is known to be susceptible to *Ichthyophonus* infections (Gregg et al., 2016; Johnstone, 1913; Murchelano et al., 1986; Sproston, 1944), but the prevalence has not been extensively monitored. A few studies indicate differences between geographic areas, seasons and individual shoals of mackerel. Sproston (1944) observed varying *Ichthyophonus* sp. (as *I. hoferi*) prevalence across different catches in the North Sea, ranging between 0% and 100% over a 3-year period with annual means of 38–70%, whereas Rahimian (1998) did not find any infected mackerel during a survey in the adjacent Skagerrak and Kattegat. Murchelano et al. (1986) observed infected individuals both in the eastern and western North Atlantic, but the general prevalence could not be determined due to low sample sizes. The diverging results of these studies indicate large differences in the prevalence of *Ichthyophonus* infections in Atlantic mackerel, possibly due to temporal fluctuations or variations in infection pressure in different geographic regions. Recent studies indicate frequent intermixing between the different spawning components within the Northeast Atlantic (NEA) mackerel stocks (Henriksen, Nøttestad, Olafsdottir, Slotte, & Sánchez, 2020; Jansen & Gislason, 2013), and infected individuals in some components may thus potentially spread parasites to other spawning components. NEA mackerel is also found increasingly further north and west, most likely due to changes in the migration pattern following climate change (Nøttestad et al., 2016; Nøttestad et al., 2020). Parasites infecting the mackerel, such as *Ichthyophonus* spp., can thus potentially spread and infect new fish host species with little or no inherent resistance to them, which could have great ecological and commercial ramifications. The diversity and prevalence of *Ichthyophonus* sp. in NEA mackerel should be monitored closely. The present study details our observations of the prevalence of *Ichthyophonus* infections in mackerel obtained from the Northeast Atlantic.

A total of 960 NEA mackerel were sampled during research cruises and from commercial catches in the North, Norwegian and Greenland Seas in 2019–2021. To assess the prevalence of *Ichthyophonus* sp., freshly caught or defrosted fish were examined macroscopically for visible signs of infection in the form of granulomas in the heart, kidney, spleen or red muscle tissue (Hodneland

TABLE 1 Prevalence of *Ichthyophonus* infections in catches of NEA mackerel from 2019–2021, tentatively observed macroscopically or microscopically as resting spores or hyphae in the heart, spleen, kidney or red muscle tissue

Cruise no./catch no.	Date	Geographical area	Coordinates (Decimal)		Fishing method	Research/commercial catch	Notes on examination	#of tentatively positive fish/#fish examined (percentage infected %)	
			Latitude °N	Longitude °E				Macroscopic[a]	Microscopic[b]
2019856/1[e]	08.06.19	North Sea	58.25	3.34	Purse seine	Commercial	Bycatch of mackerel from herring fishing	11/22 (50%)	11/11[c]
2019853/1[e]	02.10.19	North Sea	59.31	−0.63	Purse seine	Commercial	Examined fresh	16/22 (73%)	14/16[c]
2019854/1[e]	11.10.19	North Sea	59.02	−0.47	Purse seine	Commercial	Stored cold in tank (~2°C), examined 13.10.2019	25/30 (83%)	ND
2020811/1	04.06.20	North Sea	59.80	2.68	Purse seine	Commercial	Bycatch from herring fishing, stored cold in tank (~2°C), examined 06.06.2020	19/36 (52%)	ND
2020814/37582	30.07.20	Greenland Sea	74.92	5.51	Trawl	Research	Stored frozen until examination	63/100 (63%)	31/50 (62%)[d]
2020808/1	09.10.20	North Sea	58.98	−0.82	Purse seine	Commercial	Macroscopic examination on fresh fish, microscopic examinations on tissue stored frozen	51/100 (51%)	21/30 (70%)[d]
2020816/37451	01.07.21	Norwegian Sea	61.33	4.23	Trawl	Research	Examined fresh	20/25 (80%)	ND
2020816/37453	02.07.21	Norwegian Sea	61.33	1.09	Trawl	Research	Examined fresh	17/25 (68%)	ND
2020816/37454	02.07.21	Norwegian Sea	61.28	−0.97	Trawl	Research	Examined fresh	20/25 (80%)	ND
2020816/37457	03.07.21	Norwegian Sea	61.52	−4.01	Trawl	Research	Examined fresh	25/25 (100%)	ND
2020816/37460	04.07.21	Norwegian Sea	62.23	−3.05	Trawl	Research	Examined fresh	21/25 (84%)	ND
2020816/37462	04.07.21	Norwegian Sea	62.18	0.09	Trawl	Research	Examined fresh	22/25 (88%)	ND
2020816/ 37465	05.07.21	Norwegian Sea	63.93	6.63	Trawl	Research	Examined fresh	18/25 (72%)	ND
2020816/37467	06.07.21	Norwegian Sea	63.95	4.38	Trawl	Research	Examined fresh	17/25 (68%)	ND
2020816/37469	06.07.21	Norwegian Sea	63.90	−0.20	Trawl	Research	Examined fresh	18/25 (72%)	ND
2020816/37473	07.07.21	Norwegian Sea	64.36	−1.90	Trawl	Research	Examined fresh	20/25 (80%)	ND
2020816/37476	08.07.21	Norwegian Sea	64.77	0.91	Trawl	Research	Examined fresh	18/25 (72%)	ND
2020816/37479	09.07.21	Norwegian Sea	64.79	3.19	Trawl	Research	Examined fresh	18/25 (72%)	ND
2020816/37480	09.07.21	Norwegian Sea	65.58	9.26	Trawl	Research	Examined fresh	21/25 (84%)	ND
2020816/37491	11.07.21	Norwegian Sea	65.67	2.04	Trawl	Research	Examined fresh	14/25 (56%)	ND
2020816/37493	12.07.21	Norwegian Sea	65.55	−2.85	Trawl	Research	Examined fresh	23/25 (92%)	ND

TABLE 1 (Continued)

Cruise no./catch no.	Date	Geographical area	Coordinates (Decimal)		Fishing method	Research/commercial catch	Notes on examination	#of tentatively positive fish/#fish examined (percentage infected %)	
			Latitude °N	Longitude °E				Macroscopic[a]	Microscopic[b]
2020816/37496[e]	14.07.21	Norwegian Sea	67.36	−0.55	Trawl	Research	Examined fresh	22/25 (88%)	ND
2020816/37498	14.07.21	Norwegian Sea	67.40	2.01	Trawl	Research	Examined fresh	23/25 (92%)	ND
2020816/37500	16.07.21	Norwegian Sea	67.28	9.53	Trawl	Research	Examined fresh	24/25 (96%)	ND
2020816/37501	16.07.21	Norwegian Sea	67.22	11.74	Trawl	Research	Examined fresh	20/25 (80%)	ND
2021810/1	28.08.21	Norwegian Sea	63.72	2.93	Purse seine	Commercial	Examined after storage in tank (~2°C) appr. 48 h, followed by storage on deck (~10°C) appr. 24 h	8/25 (32%)	13/25 (52%)
2021810/2[e]	31.08.21	Norwegian Sea	61.99	1.69	Purse seine	Commercial	Fresh, examined after storage on deck (~10°C) for appr. 24 h	32/50 (64%)	34/50 (68%)
2021810/3	02.09.21	Norwegian Sea	63.36	1.42	Purse seine	Commercial	Fresh, examined immediately (1–8 h) after catch	34/50 (68%)	32/50 (64%)
2021810/3	02.09.21	Norwegian Sea	63.36	1.42	Purse seine	Commercial	Fresh, examined 18–21 h after catch	15/25 (60%)	19/25 (76%)
2021811/1	26.10.21	Norwegian Sea	63.01	4.54	Purse seine	Commercial	Stored frozen immediately after catch, thawed on deck (~10°C) for 48 h prior to examination	24/25 (96%)	24/25 (96%)

Note: Samples were obtained either from dedicated research cruises, or from research studies investigating fish obtained from commercial catches.

Abbreviation: ND, not determined.

[a]Visible granuloma containing resting spores in heart, spleen or kidney.

[b]Resting spores and/or hyphae observed microscopically in heart, spleen or kidney.

[c]Only samples positive for macroscopic signs were examined with microscopy.

[d]Random selection of samples examined regardless of macroscopic results.

[e]Tissue transplant cultures from these catches were used for genetic identification.

et al., 1997; Sproston, 1944). Moreover, the spleen and kidney of either all fish or a random sub-sample of fish from selected catches (see Table 1 for details) were examined microscopically for the presence of granulomas with thick-walled multinuclear bodies in the granulomas, generally called 'resting spores' (Okamoto et al., 1985) or schizonts (Kocan, 2013), and hyphae described by Meyers et al., (Meyers et al., 2019). Macroscopic observations of resting spores (Figure 1a–d, Table 1) indicated 32%–100% *Ichthyophonus* sp. prevalence in individual batches (Table 1). Further microscopic observations of resting spores and hyphae in spleen and kidney confirmed this finding (Figure 1e–g, Table 1).

In July 2021, samples for histology were prepared from internal organs and muscle tissue from selected NEA mackerel showing macroscopic signs of infections. The tissues were preserved on 4% formaldehyde (pH 6.9) and stained with haematoxylin-erythrosine saffron (HES) or periodic acid-Schiff (PAS).

Resting spores and hyphae observed microscopically were similar in size and appearance to those observed in NEA mackerel by Sproston (1944), and the histological sections showed the presence of typical *Ichthyophonus* sp. resting spores in the examined tissues (Figure 2). There were some differences in the microscopic observations depending on the time between catching and analysing the fish, and between fresh fish and fish that was stored frozen. In fresh fish examined within 1–8 h post catch, resting spores were visible while hyphae were not seen. However, some resting spores showed early signs of germination (Figure 1e–f). Hyphae, observed either as hyphal tips protruding from resting spores or as free hyphae in the tissues (Figure 1g), were mainly found in fresh fish examined >18 hours post mortem (Figure 3). In many instances, evacuated hyphae remained attached to the parental resting spore by a hyphal thread (Figure 1g). In fish examined 18–30 h post catch, hyphae were observed in most tissues harbouring resting spores (Figure 3). The observed lag in post mortem hyphal growth is consistent with the findings of Rahimian (1998) on infected herring, and may suggest that biochemical processes or changes in pH in the tissues trigger germination. Still, some fish examined >18 h post mortem contained resting spores only, with no hyphae or signs of germination being observed. It is unclear if these tissues contained predominantly ungerminated or dead spores.

Several bacteria and parasites can induce granuloma formation in fish that superficially resemble *Ichthyophonus* infections (Kocan et al., 2004; Murchelano et al., 1986), for example, *Mycobacterium* spp. which commonly occur in Atlantic mackerel (Murchelano et al., 1986). A study of Northwest Atlantic mackerel from New Jersey coastal waters found that 39% of the mackerel (N = 91) contained granulomas in the kidneys, but only 5% contained identifiable *Ichthyophonus* sp. stages (Murchelano et al., 1986). The currently most accurate method for confirming *Ichthyophonus* infections is through cultivation of infected tissues in selective growth media (Richard Kocan et al., 2011) or using PCR- or

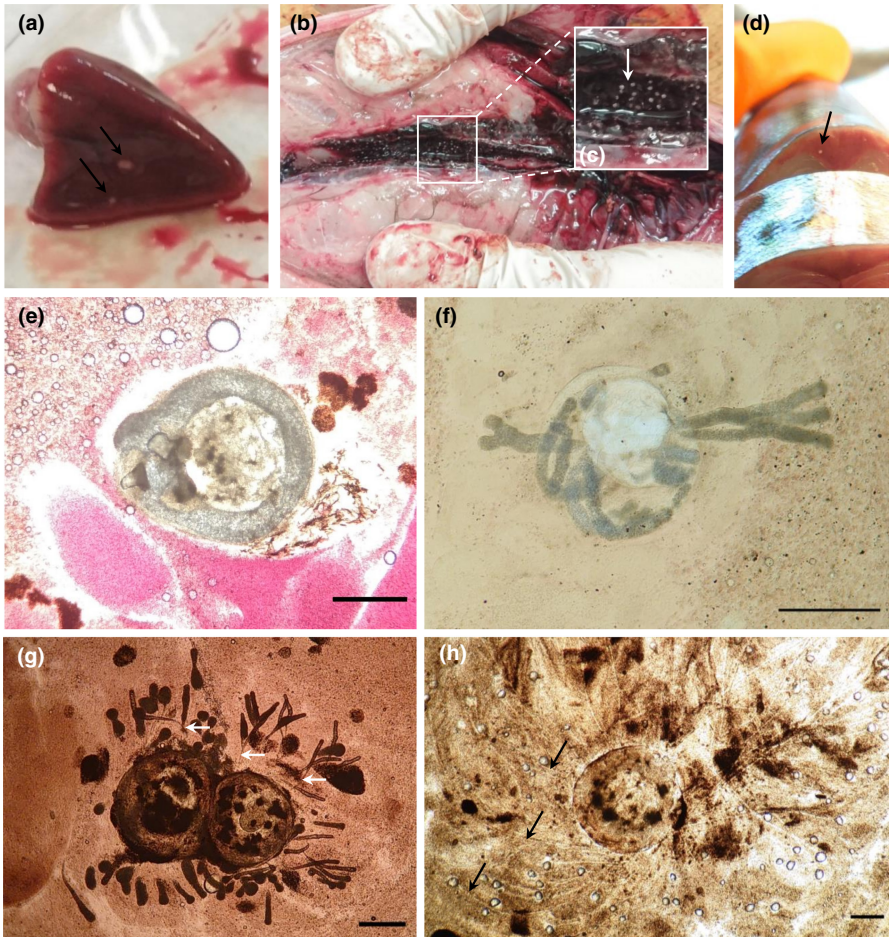

FIGURE 1 Macroscopic and microscopic signs of *Ichthyophonus* infection in NEA mackerel. Macroscopic signs seen as granulomas (arrows) on the heart (a), kidney (b,c) and in the red muscle (d). Microscopic signs of infection seen as granulomas containing resting spores, germinating resting spores and short hyphae in the kidney of fresh fish (e–g). (e–f) The first signs of germinating resting spores, approximately 8 h post mortem. (g) More advanced germination approximately 20 h post mortem. Arrows indicate evacuated hyphal tubes connecting the hyphae to the resting spores. (h) Kidney after freezing, with resting spore and connected hyphal tubes (arrow) and degraded hyphae. All scalebars are 250 μM

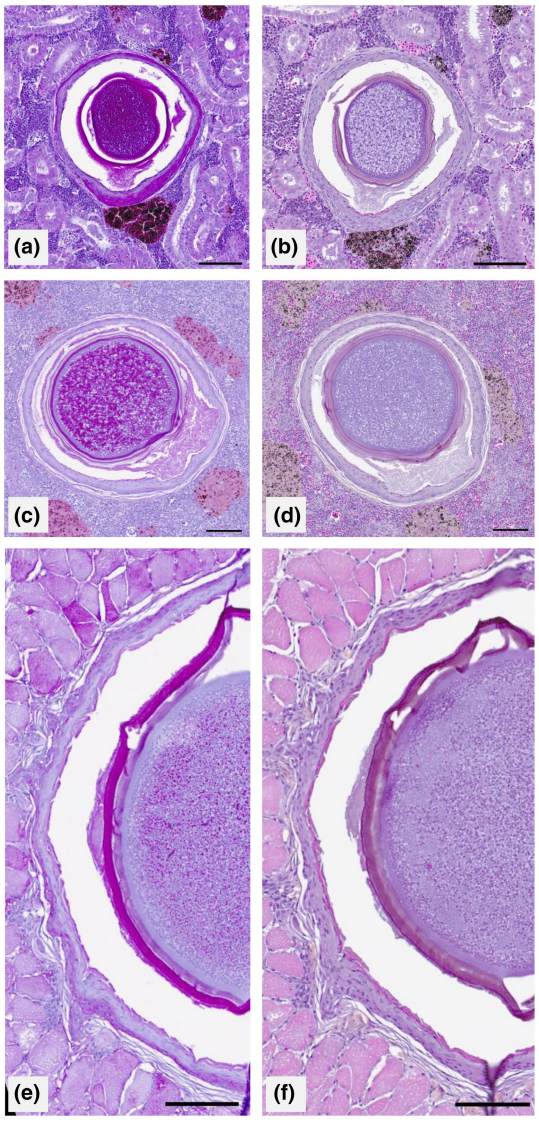

FIGURE 2 *Ichthyophonus* resting spores in NEA mackerel tissues. PAS- (a) and HES-stained (b) resting spore in kidney, spleen (c, d) and muscle tissue (e,f). All scalebars are 100 μM

qPCR-based assays (White et al., 2013). However, these methods can be very time-consuming and are not always feasible during routine examinations of large numbers of fish. In addition, PCR-based methods do not separate between living and dead parasites. An alternative method for detecting infections in NEA mackerel is to examine small pieces of the kidney and spleen for the presence of hyphal growth. No other histozoic marine fish parasites or fungi produce the hyphal growth seen in *Ichthyophonus* sp. The presence of aseptate hyphae in combination with resting spores in NEA mackerel tissues is therefore highly indicative of infection with live *Ichthyophonus* sp.

In August/September 2021, 50 and 75 fresh fish were examined microscopically at 1–8 and 18–30 h intervals post mortem (Table 1, Figure 2). Of 50 fish examined at 1–8 h, 33 displayed resting spores only, with a single mackerel showing signs of early hyphal growth (Figure 2). In the fish examined 18–30 h post mortem, resting spores were observed in 47 and 71 fish macroscopically and microscopically, respectively, whereas *Ichthyophonus* hyphae were observed in 43 of the fishes. Thus, 91% of mackerel displaying macroscopic signs of infection (granulomas with resting spores) also contained hyphae in the spleen and/or kidney, indicating that the majority of fish displaying granulomatous tissues were infected with *Ichthyophonus* sp.

Ichthyophonus resting spores do not survive prolonged freezing at −20°C (Athanassopoulou, 1992), and mackerel stored frozen in the present study only displayed hyphae in a few cases, most likely where freezing was delayed, allowing germination prior to freezing. Thus, hyphae were almost exclusively observed in fresh fish, that is, not previously frozen. Those hyphae seen in frozen mackerel often appeared evacuated, seemingly having lost their typical shape (Figure 1g). Such hyphae may easily be overlooked if not connected to a resting spore, making the observations less accurate. Granulomas, on the other hand, are readily observable in frozen fish, but can be confused with other parasitic or bacterial infections. Therefore, we considered microscopic detection of hyphal growth in the kidney and spleen of fresh fish, approximately 18–30 hours post catch, to be most reliable for detecting *Ichthyophonus* infections in the mackerel.

To confirm *Ichthyophonus* sp. presence and reveal the genotype, samples for tissue transplant cultures were taken from heart or muscle tissue of randomly selected, freshly caught mackerel (see Table 1). Samples were cultured in Tris-buffered MEM-media (Gibco™) contaning 5% fetal bovine serum at pH 7–9 or 2–3.5 as described by Okamoto et al. (1985) and Kocan et al., (2004), and kept at 15°C for 7–14 days prior to examination. Cultures that showed growth resembling *Ichthyophonus* sp. with spherical, multinucleate bodies growing from the tissue-samples, were confirmed by PCR and sequencing to be *Ichthyophonus* sp. based on their 18S ribosomal genes. Primers IchEK-F1 5′-ACCCGACTTCTGGAAGGGTTGT-3′ (a modified PIchF1 primer (White et al., 2013) and MesR1 5′-GCTTACT AGGAATTCCTCGTTGAAGA-3′ designed by EK were used with PCR settings: 5 min at 95°C, followed by 35 amplification cycles at 30s-95°C, 1 min-58°C, 1 min-72°C, followed by 7 min at 72°C. Sanger sequencing was done by Eurofins Genomics (Cologne, Germany). The resulting five sequences were identical and showed >99% similarity with *Ichthyophonus* sp. 18S rRNA gene sequences in GenBank® originating from rainbow trout and Alaska pollock (*Gadus chalcogramma*). Sequences obtained in this study are available in GenBank under accession no. OM869424-OM869428.

Melanomacrophage assemblies were observed in close association with granulomas in the kidney and spleen indicating an immune response by the fish (Figure 1f–g), but overall, infected fish did not differ significantly in Fulton's condition factor K ($K = 100 \times \text{Length}^3(\text{cm})/\text{Weight (g)}$; T-test, $p = .45$) from uninfected fish (Table 2). Hence, we found no signs of *Ichthyophonus* sp. being particularly pathogenic to NEA mackerel. A study on *Ichthyophonus* in Pacific halibut in North America found a similar pattern, with high prevalence but seemingly low pathogenic infections (Hershberger et al., 2018). In contrast, studies of *Ichthyophonus* in Pacific herring, Atlantic herring and American

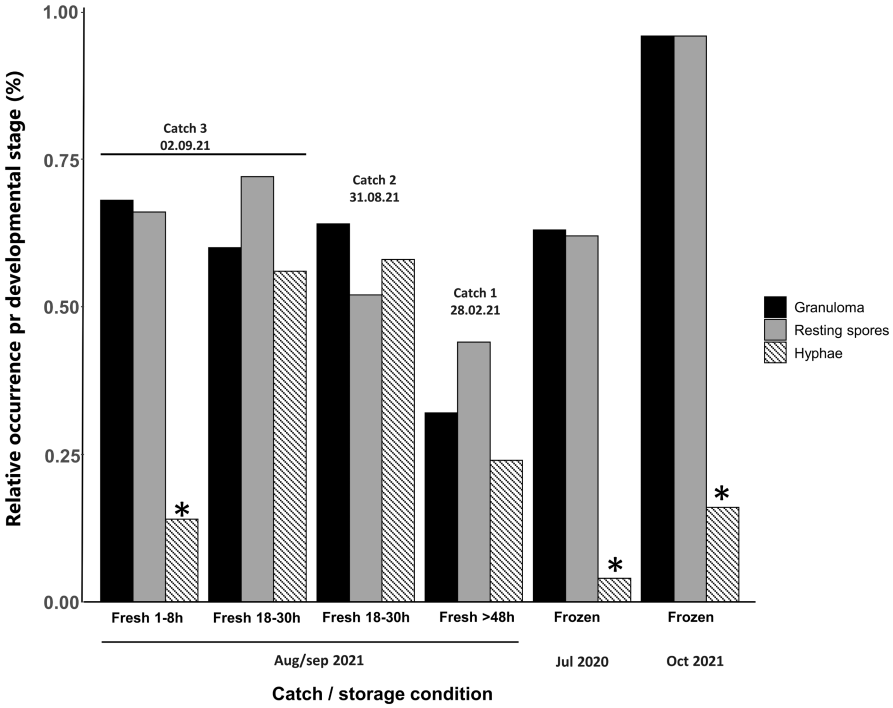

FIGURE 3 Macroscopic observations of granuloma and microscopic observations of resting spores and hyphae examined in fresh or previously frozen spleen and kidney of NEA mackerel at different time intervals post catch. * indicates that most hyphae observed were at an early germination stage, as seen in Figure 1e

TABLE 2 Descriptive statistics of mackerel length (cm) and weight (g) used to calculate Fulton's K. Results included are from microscopic examinations

	Length (cm) and weight (g)			
Variable	Mean	Minimum	Maximum	Std.dev.
Uninfected fish $N = 95$				
Length	35	21	40	2.7
Weight	340	206	645	93.5
Infected fish $N = 197$				
Length	36	30	55	2.9
Weight	440	193	692	97.3

shad (*Alosa sapidissima*) indicated that *Ichthyophonus* infections can be detrimental to host health (Richard Kocan et al., 2006; Marty et al., 1998) or may cause high mortalities (Rahimian & Thulin, 1996). This could be due to different immune responses in different fish species, with some hosts having higher level of tolerance to *Ichthyophonus* infections. Another possibility is that different strains or species of *Ichthyophonus* infect different fish species, and that *Ichthyophonus* sp. in NEA mackerel is less pathogenic than *Ichthyophonus* species infecting other fish hosts.

Future work should explore the species diversity and differences in host specificity between *Ichthyophonus* sp. infecting NEA mackerel and the strains or species that infect other fish. The migration pattern of NEA mackerel is changing rapidly, being found increasingly further north and west (Nøttestad et al., 2016; Nøttestad et al., 2020). Therefore, parasites such as *Ichthyophonus* spp. can be transported further north, potentially spreading to new naïve fish host species with little or no resistance to them. As the Arctic Ocean continues to warm up, *Ichthyophonus* should be monitored closely.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made openly available in the Norwegian Marine Data Centre (https://nmdc.no/) upon publication, and a DOI will then be attached to the final version of the document.

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